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5.—The Physiology of Sclerophyll Plants

Presidential Address, 1953

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The physiology of sclerophylls growing in areas of Mediterranean type climate throughout the world is reviewed. Particularly in so far as their water economy is concerned there is evidence that such sclerophylls differ markedly from the xerophytes and mesophytes of the type studied by Maximov at Tiflis. The available data on the origin and function of xeromorphic characters in sclerophylls is also examined and the need for further research to clarify the position here is stressed.

Introduction

The publication of "Die Pflanzenwelt von West Australien" by Diels in 1906 following his visit in 1901-1902 forms one of the major landmarks in the botanical history of Western Australia. Diels, trained at a time when Schimper's "Plant Geography upon a Physiological Basis" (1898, 1903) was profoundly influencing botanical thought, not only gave due weight to the floristic side (as expressed in "Fragmenta Phytographiae Australiae occidentalis" (1905) which he published jointly with Pritzel) but also laid the foundations of plant geography and ecology. Within the framework of his introductory account of the elements of the vegetation of the whole continent, the picture of the vegetation of South Western Australia stands out in clear relief. It is to Diels that we owe, among other things, the delimitation of the South Western and Ereman botanical provinces, the characterisation of the overall vegetation formation, the first coherent account of the plants which determined the physiognomy of the vegetation, and a basic discussion of the growth forms and of the peculiarities of leaf morphology and structure of South Western and marginal Ereman vegetation types.

Using the nomenclature of the time, Diels characterised most of the hard-leaved evergreen vegetation as being xerophytic. The leaves were

observed to be modified in a variety of ways from the usual conception of a normal soft mesomorphic leaf characteristic of plants growing in temperate regions of the northern hemisphere. These modifications together with the pale dull-green or grey appearance of many of the leaves gave, he considered, a distinctive look to Australian vegetation. This same feature is characteristic of course of hard-leaved evergreen vegetation throughout the world, whether it be the South West part of the Cape region of South Africa, the Mediterranean countries, California or Central Chile. The term *sclerophyll*, coined by Schimper (1903) applies very aptly to this kind of vegetation. Diels described and classified the various kinds of sclerophylls in the West Australian area under the headings of Moderate Sized Sclerophyll leaves, Ericoid leaves and Needle-like leaves. He also emphasized the importance of the condition of aphyllly in the Western Australian sclerophyll vegetation pointing out many instances where winged stems took over the functions of the leaf. Adamson and Osborne (1924) described and classified the sclerophylls of South Australia. They used the term Broad Leaf Sclerophyll while retaining the Ericoid and Needle-leaf types. Patton (1932) described similar sclerophyll leaf types in Victoria. The various morphological and structural modifications characteristic of Australian sclerophylls are set out in Table I. By virtue of possessing these modifications they are described as being *xeromorphic*. This descriptive term is used because such characters are commonly present in vegetation which grows in dry localities and distinguishes it from the vegetation of moister more temperate areas which lack them. The possession of xeromorphic modifications is not, of course, peculiar to sclerophylls. The Australian tomentose succulents for example, also show xeromorphic characters and together with sclerophylls they are referred to as *xeromorphs*.

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TABLE I

Morphological and Structural Modifications Characteristic of Australian Sclerophylls

Illustrated with Examples from Western Australia

Broad and leathery leaves	Spiny stems
<i>Stirlingia latifolia</i>	<i>Cryptandra parvifolia</i>
<i>Conospermum scaposum</i>	<i>Psammomoya ephedroides</i>
<i>Banksia grandis</i>	
<i>Eucalyptus marginata</i>	Sunken stomata
<i>Acacia cyanophylla</i> (phyllode)	<i>Hakea clavata</i>
	<i>Acacia acuminata</i>
	<i>Daviesia pachyphylla</i>
Microphyllly—the Ericoid leaf	
<i>Micromyrtus imbricata</i>	Cutinization and lignification
<i>Astroloma macrocalyx</i>	<i>Eucalyptus</i> spp.
<i>Bossiaea eriocarpa</i>	<i>Hakea</i> spp.
<i>Hibbertia hypericoides</i>	<i>Daviesia</i> spp.
Acicular or Needle Leaf	
<i>Grevillea acerosa</i>	Development of tannins and resinous substances
<i>Hakea recurva</i>	<i>Hakea varia</i>
<i>Hovea pungens</i>	<i>Acacia acuminata</i>
	<i>Dodonaea viscosa</i>
Aphyllly	
<i>Hibbertia conspicua</i>	Strong development of palisade mesophyll and
<i>Bossiaea leptacantha</i>	weak development of spongy mesophyll
<i>Daviesia aphylla</i>	<i>Eucalyptus marginata</i>
Winged stems	
<i>Acacia alata</i>	Presence of hairs and scales or waxy bloom on
<i>Sphaerolobium alatum</i>	surface
<i>Trachymene compressa</i>	<i>Lachnostachys verbascifolia</i>
	<i>Eucalyptus caesia</i>

Interest has long centred around the question as to whether the xeromorphic modifications of sclerophylls (and of other plants in arid or semi-arid areas) have physiological significance for survival and distribution. This paper reviews the available data on peculiarities of physiology in sclerophylls with special reference to Australian vegetation, and endeavours to ascertain to what extent they are related to the characters of morphology and structure associated with the sclerophyll habit. The structural features were early held to affect the water relations of sclerophylls and much study has been devoted to this point. The first section therefore deals with their water relations. This is followed by an examination of their assimilation, respiration and general metabolism, leading on to a discussion of theories of the significance and origin of the sclerophyll habit and xeromorphic characters.

The Water Relations of Sclerophylls

Transpiration

Probably the most typical and certainly the most highly developed sclerophyll vegetation in the world occurs in parts of Australia, and the study of its physiology has engaged the attention of several botanists. Using a potometer method Wood (1923) in South Australia studied the transpiration of *Eremophila scoparia*, *Geijera parviflora* and *Casuarina lepidophloia* during summer in a 9.2 inch rainfall area at Dilkera, 90 miles north of Adelaide. He observed (see Table II) that the rates of water loss were

not high in *Eremophila* or *Geijera* and that they did not respond readily to changes in environmental conditions. In *Casuarina* the rate was definitely higher and more subject to fluctuations in evaporating power of the air. Wood concluded that the higher rate of transpiration in *Casuarina* during the day and its correspondence to the curve for evaporation was due to the ability of high winds, common in the area, to sweep along the line of stomates in the furrows of the branchlets. For *Eremophila* and *Geijera* the reduction in transpiration was ascribed to their xeromorphic modifications and the presence of vapours from oily secretions. Working in a somewhat more arid area at Curramona (250 miles north-east of Adelaide) with a rainfall of only 7.0 inches, Wood (1924) obtained additional information on the transpiration rates of sclerophylls and of a mesomorph (*Senecio magnificus*) (see Table II). The rate of water loss from the mesomorph which was growing where water was available, was much greater than that of the three sclerophylls listed. Of the three sclerophylls, the less thickly cutinised *Acacia victoriae*, which grows in water courses and swampy areas, transpired more rapidly than *Acacia aneura* and *Eremophila glabra* with their more pronounced structural modifications.

Additional results (see Table II) were obtained by Wood (1934) at Koonamore (8.4 in. rainfall) and in the Mount Lofty Ranges (20-40 in. rainfall). It may be noted that the rates of transpiration in the Mount Lofty experiments are much higher than those recorded in summer for sclerophyll plants growing in the more arid

areas at Dilker, Curnamona and Koonamore, although the rate of evaporation is lower in the ranges. This higher transpiration rate may be referable to more abundant soil moisture at the time (not reported) when these experiments were performed.

In this paper Wood (1934) used the concept of *Relative Transpiration* so that he could compare his results with those of other workers. He concerned himself more with the mean relative transpiration of the group rather than with that of individual plants and came to the conclusion that sclerophyll plants in South Australia and high moor plants in Germany (Firbas, 1931) showed no significant difference in transpiration when the relative transpirations were compared by the difference of their means.

At Melbourne in Victoria, Wilson (1924) studied the rates of water loss (using a weighing method) from intact seedling sclerophyll plants growing in pots. The aim of this work was to determine whether such plants could modify water loss, particularly during hot north wind days. He concluded that provided the available water supply was adequate, the plants had no special powers of accommodation, the rates of transpiration being quite high over long periods (see Table II). Wilson's results indicate a very high rate of water loss for sclerophylls under the conditions of his experiments. In this connection it may be noted that Henrici (1937) in South Africa, found that potted xerophytic plants could display a very high transpiration rate, but in plants tested in the field the rate was much lower. Wilson's results therefore can not be considered as being typical for field conditions in summer. The author (1946-1947) carried out experiments on sclerophylls in various parts of Victoria: Mallee country, heathland near Melbourne, Mt. Macedon and the Bogong High Plains. Results (Table II) consistently showed much lower rates of transpiration for all the sclerophylls tested than those recorded by Wilson.

Experiments on transpiration of Western Australian sclerophylls in the Perth area in late summer have also been carried out by the author during the period 1949 to 1953. Typical results obtained are shown in Table II. Restriction of transpiration occurred in sclerophylls as the dry season advanced. A mesomorph growing in the area (*Erechthites hispidula*) showed a considerably higher rate of water loss before it eventually wilted permanently and died.

Many investigations on the transpiration of sclerophylls have been made in other parts of the world, notably in the Mediterranean area, in South Africa and in California. A summary of the results of this work recalculated where necessary in mg./sq. dm./min. or mg./g./min. is presented in Table III.

Guttenberg (1907) using a weighing potometer method studied the transpiration of sclerophylls on the island of Lussin off the Yugoslav Adriatic coast. He reported then that in summer transpiration was not greatly reduced although later (1927) he modified his view. Study of his 1907 results shows that a considerable reduction in rate does in fact occur on passing from the spring to the summer and also that (particularly

when his results are recalculated in terms of the area of both sides of the leaf in certain cases) the rates are relatively low in summer.

Cooper (1922) working in California made preliminary observations on the rate of water loss in broad sclerophyll (Chaparral) during summer (Table III). While the results given are limited it may be noted that the values are relatively low.

Oppenheimer (1932) investigated the water economy of sclerophylls in the Palestine area (Table III) and showed that there was a marked restriction of transpiration during the hot and dry summer months, this restriction being associated with a state of more or less pronounced physiological rest.

Rouschal (1938) made a thorough study of the water relations of Maquis sclerophyll vegetation of Rovigno on the north eastern Adriatic coast.

He placed Maquis plants in three categories in so far as transpiration was concerned: those with low transpiration rate under all conditions, those which limit their transpiration with increasing dryness (a large group), and those with high transpiration under favourable conditions. From a study of his data it appears that transpiration, though high under favourable conditions showed reduction in all cases as the dry season advanced (Table III). Results in several cases were comparable to those of Guttenberg and Oppenheimer.

Montemartini (1930) in Italy also worked with representative Maquis plants and his results for *Ceratonia* and *Nerium* indicated that Maquis sclerophylls in general showed a parallelism between their transpiration rate and physiological activity.

Killian (1932) investigated the rates of transpiration in Algerian Maquis and found that in typical sclerophylls transpiration during the dry season was low and regular while in mesomorphic plants it was considerably higher.

Henrici (1940) at Pretoria in South Africa, compared the rates of water loss from sclerophylls and mesomorphs growing in the same area. She found that the average rate of loss in sclerophylls was relatively low while that in associated mesomorphs was much higher (Table III).

Poljokoff (1946) in Palestine closely examined the water economy of the sclerophylls *Ceratonia* and *Olea* and showed that transpiration was relatively low and regular throughout the dry season. By contrast the loss of water from a mesomorphic plant (almond) growing in the area was strikingly high (Table III).

Eckardt (1952) studied the transpiration of Garrigue vegetation (a modified form of sclerophyll) in the Narbonne (Mediterranean) region. All the species he worked with showed considerable reduction of transpiration during the dry period.

The work on transpiration in the central and eastern Mediterranean areas was reviewed by Oppenheimer (1951) who pointed out that the average transpiration in summer for the Maquis type of vegetation seldom rose above 5 mg./g./min., while that of mesomorphs growing in these areas was strikingly higher.

TABLE II

Rate of Transpiration in Sclerophylls in Australia

Name of Investigator.	Location.	Date of Experiment	Method	Test Plants	Average Rate ‡ mg./ sq.dm./ min.	Maximum Rate mg./ sq.dm./ min.	Average Rate mg./ g./min.
Wood* (1923)	Dilkera, Sth. Aust. (9.2 in. rainfall)	May (near end of five month's drought period)	Potometer	<i>Eremophila scoparia</i> .. <i>Geijera parviflora</i> .. <i>Casuarina lepidophloia</i> .. Atmometer	1.15 0.36 2.25 111.1	1.67 (2-3 p.m.) 0.55 (2-3 p.m.) 4.45 (2-3 p.m.)
Wood* (1924) ..	Curn mona Sth. Aust. (7.08 in. rainfall)	Summer	Potometer	<i>Eremophila glabra</i> .. <i>Acacia aneura</i> <i>Acacia victoriae</i> <i>Senecio magnificus</i> (mesomorph) Atmometer	0.85 1.38 4.75 15.70 223.0	1.46 (2-3 p.m.) 2.23 (2-3 p.m.) 8.86 (2-3 p.m.) 23.0
Wood* (1934)	Koonamore Sth. Aust. (8.4 in. rainfall)	Potometer	<i>Casuarina lepidophloia</i> .. <i>Geijera parviflora</i> .. <i>Eremophila scoparia</i> .. Atmometer	1.50 0.32 0.94 75.0 †
				<i>Eremophila glabra</i> .. <i>Acacia aneura</i> <i>Acacia victoriae</i> Atmometer	1.03 0.91 2.68 108.0 †
Wood* (1934)	Mount Lofty Ranges, Sth. Aust. (20-40 in. rainfall)	Weighing of cut shoots	<i>Eucalyptus leacoxylon</i> .. <i>Acacia pycnantha</i> .. <i>Hakea rugosa</i> <i>Leptospermum myrsinoides</i> .. <i>Calythrix tetragona</i> .. <i>Hibbertia stricta</i> Atmometer	26.60 25.40 21.80 7.00 8.65 12.18 87.1
Wilson* (1924)	Melbourne, Victoria (25.5 in. rainfall)	February (late summer)	Interval weighing of intact seedlings in pots	<i>Banksia serrata</i> .. <i>Eugenia smithii</i> .. Atmometer (free water surface) <i>Casuarina luehmanni</i> .. <i>Acacia pycnantha</i> .. <i>Eucalyptus macrorrhyncha</i> ..	58.3 21.8 180.7 40.3 17.5 15.2
Grieve (hitherto unpublished data)	Walpeup, Victoria (Mallee) (10-12 inches rainfall)	September, 1946	Potometer ..	<i>Eucalyptus dumosa</i> .. <i>Eremophila glabra</i> .. <i>Acacia ligulata</i> <i>Heterodendron oleifolium</i> (herbaceous xerophyte) Atmometer	5.5 3.3 1.8 1.3 86.0	10.0 3.6 2.0 2.7 118.0
Do. do	Bogong High Plains, Victoria	January, 1947 (Summer)	Potometer	<i>Eucalyptus gigantea</i> .. <i>Acacia falciformis</i> .. Atmometer	4.1 4.0 86.1
Do. do.	Mt. Macedon, Victoria	February, 1947	Potometer	<i>Eucalyptus gigantea</i> .. <i>Acacia melanoxylon</i> (gully plant) Atmometer	6.3 2.0 78.0	12.7
Do. do.	Oakleigh-Frankston, Victoria, (Sandheath). (25.5 in. rainfall)	February, 1947	Rapid weighing	<i>Banksia collina</i> .. <i>Leptospermum laevigatum</i> .. <i>Hibbertia sericea</i> .. <i>Platglobium obtusangulum</i> .. Atmometer (Filter paper "leaf")	4.0 1.1 3.5 2.2 25.0
Do. do.	Perth area, Western Australia, (32-34 in. rainfall)	1950 (late summer)	Rapid weighing	<i>Hibbertia hypericoides</i> .. <i>Bassia eriocarpa</i> .. <i>Casuarina fraseriana</i> .. <i>Conostephium pendulum</i> .. <i>Eucalyptus calophylla</i> .. <i>Hardenbergia comptoniana</i> .. <i>Stirlingia latifolia</i> .. <i>Banksia attenuata</i> .. <i>Erechthites hispidula</i> (mesomorph) Atmometer (Filter paper "leaf") 7.8 1.2 5.8 8.3 15.8 42.0	2.2 0.3 2.9 2.8 4.2 1.3 2.3 4.2 13.3 31.4

* Values recalculated to mg./sq.dm./min. (1923, 11 a.m.-6 p.m.), (1924, 8 a.m.-4 p.m.).

† Actual values in Wood's paper x 10.

‡ Transpiration rate is given in mg./sq.dm./min. for the total area of test leaves (cf. Rouschal, 1938).

Examination of the results in Table III shows that this holds true also for the sclerophylls of the western end of the Mediterranean and for those of South Africa and California. For typical sclerophylls in Western Australia under summer conditions, the author has found average rates to be below 5 mg./g./min. Results have also been calculated as mg./sq. dm./min. to facilitate comparison with earlier work in Victoria and it would appear that results obtained by the author for sclerophylls there, are generally below the equivalent of 5 mg./g./min. Wood's results (1923, 1924, 1934) using the potometer method show an average rate below the equivalent of 5 mg./g./min. The transpiration results for sclerophylls of the Mt. Lofty area using the weighed shoot method are, however, well above Oppenheimer's average figure. These may, as indicated earlier, have shown a high transpiration rate because of favourable soil moisture conditions which would obtain if the experiments were done in late spring or early summer. In the Perth area the author

has found that rates of transpiration of sclerophylls are high during the transition period into summer but decline markedly later. Wilson's high results for well watered seedling sclerophylls growing in pots are not considered to be typical of water loss for natural growing vegetation. It is held that the author's more recent work under field conditions gives a clearer indication of the transpiration pattern for Victoria.

Summarizing the above it appears that many sclerophylls in southern Australia when studied under field conditions during the dry summer period have, as compared with mesomorphs growing in the same areas, a relatively low average rate of transpiration. The same is true of sclerophylls in other parts of the world. The question as to whether this restriction of transpiration is related to the xeromorphic modifications of sclerophylls described earlier or to other aspects of their physiology, will be returned to in a later section.

TABLE III

Rate of Transpiration in Sclerophylls of the Mediterranean Area, U.S.A. and South Africa

Name of Investigator	Location	Method	Test Plant	Average Rate*			Maximum Rate Dry Conditions
				mg./sq.dm./min.		mg./g./min.	
				Favourable Conditions	Dry Conditions	Dry Conditions	
Guttenberg (1907)	Is. of Lussin, Northern Jugoslavia, Adriatic Coast (Maquis)	Weighing Potometer	<i>Laurus nobilis</i>	2.66	1.66	
			<i>Arbutus unedo</i>	8.50	2.91	
			<i>Olea europaea</i>	3.66	3.75	
			<i>Ceratonia siliqua</i>	3.00	
			<i>Pistacia lentiscus</i>	2.50	2.16	
Cooper (1922)	California (Chaparral)	Weighing Potometer	<i>Adenostoma</i>	1.0-1.8	
			<i>Arctostaphylos</i>	0.66-1.1	
			<i>Arbutus</i>	0.5	
Oppenheimer (1932)	Palestine (Maquis)	Rapid weighing	<i>Ceratonia siliqua</i>	0.17	
			<i>Arbutus andrachne</i>	0.22	
			<i>Laurus nobilis</i>	0.37	
			<i>Prunus amygdalus</i> (mesomorph)	15.8	
Rouschal (1938)	Rovigno, N.E. Adriatic Coast (Maquis)	Rapid weighing	<i>Ruscus acutifolius</i>	1.22	1.01	mg./sq.dm./min.
			<i>Viburnum tinus</i>	5.53	1.1	2.26
			<i>Laurus nobilis</i>	4.26	0.72	2.20
			<i>Arbutus unedo</i>	6.20	2.22	1.26
			<i>Olea europaea</i>	12.80	3.39	2.91
			4.24
Henrici (1940)	Pretoria, South Africa (large Karoo bushes) (summer rainfall area)	Rapid weighing	<i>Olea verrucosa</i>	Average over all Seasons	mg./g./min.
			<i>Rhus burchellii</i>		5.33
			<i>Rhus lancea</i>		4.33
			<i>Heteromorpha arboreescens</i> (mesomorph)		3.16
			<i>Royenia microphylla</i> (mesomorph)		8.16
				7.83
Poljokoff (1946)	Palestine (Maquis)	Rapid weighing	<i>Ceratonia siliqua</i>	4.95	8.72
			<i>Olea europaea</i>	4.07	10.22
			<i>Prunus amygdalus</i> (mesomorph)	13.37	29.89
Eckardt (1952)	Narbonnalse region (Garigue)	Rapid weighing	<i>Teucrium flavum</i>	12.0	1.1
			<i>Coronilla glauca</i>	20.4	2.0
			<i>Bupleurum fruticosum</i>	9.0	1.0

* Transpiration rate is given as mg./sq.dm./min. for the total area of test leaves (cf. Rouschal, 1938).

The Rapidity of the Transpiration Stream

It is of interest to know whether there is any relationship between the rate of transpiration and the structure of the conducting elements. Huber (1932, 1937) pioneered research in this field and his methods were applied by Rouschal (1937-38) to the study of the rate of movement of the transpiration stream in Maquis plants with diffuse porous stem structure at Rovigno (see Table IV). In the moist season the average rate was 2.3 metres per hour (maximum rate 4.5 metres per hr.; minimum rate 1.5 metres per hr.), but in the late dry period it fell to 0.96 metres per hour (minimum 0.7 metres per hr.). In contrast the rates in ring porous (mesomorphic) types ranged up to 45 metres per hour.

The stem structure of selected sclerophylls in Western Australia has been studied by the author who has found them also to be of the diffuse porous type. Preliminary work on rate of movement of the transpiration stream has given results rather higher than those obtained by Rouschal for Maquis sclerophylls under similar favourable conditions. It should be noted, however, that in studying Western Australian sclerophylls only the indigo-carmin and eosin dye method has been used and not the more accurate electrical conductivity method used by Rouschal. Values obtained by the dye method are known to be rather higher than those obtained by the electrical method, so that the rates for Western Australian sclerophylls must be considered as maximum values. The average rate for three test plants in late spring was of the order of 6.6 metres per hour and for the dry period in summer, 3.5 metres per hour.

TABLE IV

The Rapidity of the Transpiration Stream in Sclerophylls in Metres per hour

Rouschal (1938) at Rovigno (Mediterranean)			Grieve, Perth, Western Australia (hitherto unpublished data)		
Plant	Moist Conditions	Dry Conditions	Plant	Moist Conditions (late spring)	Dry Conditions (late Summer)
<i>Arbutus unedo</i>	1.5	0.7	<i>Banksia attenuata</i>	7.2	5.5
<i>Laurus nobilis</i>	3.1	1.2	<i>Hibbertia hypericoides</i>	6.6	1.5
<i>Olea europaea</i>	2.4	0.7	<i>Stirlingia latifolia</i>	6.0	3.4
<i>Pistacia lentiscus</i>	2.2				
<i>Pistacia terebinthus</i>	4.5	1.5			
<i>Phillyrea media</i>	2.0	0.7			
Average	2.3	0.96	Average	6.6	3.5

Both sets of results (Table IV) confirm Huber's prediction (1935) that rates would be relatively slow in diffuse porous sclerophylls with their numerous small vessels of greater conducting area as compared with ring porous types with their larger vessels but more restricted conducting area. It may be noted also that the sclerophylls of the eastern Mediterranean area and those of Western Australia show slower rates of dye movement in summer in agreement with the reduced transpiration rates described earlier.

The Osmotic Pressures of Sclerophylls

It now seems well recognised that sclerophylls as a group have a reasonably high osmotic pressure, particularly as compared with mesomorphs.

A summary of the data now available on the osmotic pressures of sclerophylls in Australia and in different parts of the world is presented in Table V. For typical sclerophylls in the Mt. Lofty Ranges in South Australia, Wood (1934) recorded by the plasmolytic method an average value of 22 atmospheres. For more arid areas (Koonamore) he found that the average osmotic pressure was considerably higher at 54 atmospheres. Grieve and McAleer using Barger's method with expressed sap, found an average of 20 atmospheres in late summer for sclerophylls near Perth, Western Australia. Values

for sclerophylls from the more arid areas in Western Australia are not yet available for comparison with those of arid South Australia. It may be noted, however, that under similar arid conditions in Arizona, Braun-Blanquet and Walter (1931) found an average of 30 atmospheres. For the Mediterranean area (including Corsica, the Northern Adriatic coast, Palestine and Algeria) average values ranging from 22-41 atmospheres have been reported (Table V).

It appears from these results that with one or two exceptions there is reasonable correspondence in the osmotic pressures of sclerophylls in different parts of the world. Most workers are in agreement also that a rise in osmotic pressure occurs in sclerophylls as one passes from the moist to the really dry period: Rouschal (1938) showed values of 21 atmospheres at Rovigno in early summer and of 37 in late summer; Grieve and McAleer working in the Perth area noted a marked rise in osmotic pressure of the sclerophylls, *Stirlingia latifolia*, *Hibbertia hypericoides*, *Bossiaea eriocarpa* and *Banksia menziesii* in passing from spring to summer. Braun-Blanquet and Walter (1931) by contrast however, reported no significant upward change in the osmotic pressures of plants in the Montpelier region on passing from winter to summer. This region, it may be noted however, is close to the northern limit of Mediterranean sclerophylls and may not be typical.

TABLE V

Osmotic Pressures of Sclerophylls
Australia

South Australia Wood (1934) (Plasmolytic Method)		Western Australia Grieve and McAleer (unpublished data) (Barger's Method)	
(a) Koonamore (Arid) September (Spring)	(b) Mt. Lofty Ranges	Perth March (Late summer)	
<i>Acacia aneura</i> 68 atm	<i>Eucalyptus odorata</i> 30 atm	<i>Banksia menziesii</i> 21 atm	
<i>Acacia barkittii</i> 55 "	<i>Acacia pycnantha</i> 25 "	<i>Stirlingia latifolia</i> 21 "	
<i>Eremophila scoparia</i> 50 "	<i>Hibbertia stricta</i> 21 "	<i>Hibbertia hypericoides</i> 27 "	
<i>Myoporum platycarpum</i> 43 "	<i>Xanthorrhoea semi-plana</i> .. 15 "	<i>Bossiaea ericarpa</i> 21 "	
	<i>Leptospermum myrsinoides</i> .. 18 "	<i>Hardenbergia comptoniana</i> .. 14 "	
		<i>Kennedya prostrata</i> 21 "	

Mediterranean Area

	Braun- Blanquet & Walter (1931)	Oppenheimer (1932)	Killian & Faurel (1933)	Guttenberg & Buhr (1935)	Rouschal (1938)	Poliakoff (1949)	Konis (1949)	Eckardt (1952)
<i>Arbutus unedo</i>	24.0	33.2	40.6
<i>Arbutus andrachne</i>	...	31.1	26.6	...
<i>Capparis spinosa</i>	21.3
<i>Ceratonia siliqua</i>	...	20.5	20.2	16.0	...
<i>Laurus nobilis</i> ..	17.5	28.3	...	28.3	30.1	...	27.3	...
<i>Nerium oleander</i>	22.3
<i>Olea europaea</i> ..	32.5	27.0	...	51.7	46.9	29.5
<i>Phillyrea media</i>	60.2	49.5	...	40.0	...
<i>Pistacia lentiscus</i> ..	24.0	28.1	29.0
<i>Pistacia palaestina</i>	21.7	...
<i>Quercus ilex</i> ..	25.0	32.6	29.5
<i>Bupleurum fruticosum</i>	40.0
<i>Teucrium flavum</i>	37.5
<i>Coronilla glauca</i>	42.5
Mesomorphs								
<i>Roseda villosa</i>	10.5
<i>Senecio coronopifolius</i>	6.5
<i>Matthiola marocana</i>	8.0
<i>Moricandia suffruticosa</i>	8.0

Eckardt (1952), the most recent worker in this field has studied Garrigue vegetation in the French Mediterranean region, and found highly significant increases in osmotic pressures in plants with the passage from winter to summer conditions. During the wet season the average osmotic pressure of plants he tested was 13.7 atmospheres while during the dry season the average value rose to 40.7 atmospheres.

Compared with known results for mesomorphs (Maximov 1929; Killian and Faurel 1933) the values for sclerophylls are very much higher and the increasing dehydration of the protoplasm found in most instances with increasing dryness appears to be associated with decreasing transpiration rate. Boon-Long (1941) has made the suggestion that reduction in transpiration is brought about by the lowering of permeability of tissues to water consequent upon higher osmotic concentrations. Whether this is the case for sclerophylls still remains to be determined.

The Stomatal Frequencies of Sclerophylls

The question of stomatal frequency is important in relation to the effect of moist versus dry conditions on plants, but critical data is somewhat limited for sclerophylls in areas other than Australia.

Wood (1934) reported that for 39 different sclerophyll tree and shrub types in the Mt. Lofty area of South Australia, there was a stomatal frequency of 230 ± 19 . The family Proteaceae was found to have a low stomatal frequency of 145 ± 19 while the Epacridaceae (302 ± 5) had a high one as did also the families Myrtaceae (301 ± 22) and Leguminosae (277 ± 21). Sclerophylls from the same families growing in more arid areas (Koonamore) were found to show no significant difference in stomatal frequency.

Wilson (1924) determined the stomatal frequencies of well watered pot grown seedling sclerophylls at Melbourne, Victoria. Analysis of his figures by Wood (1934) showed a mean frequency of 190 ± 15 , which Wood considered did not differ significantly from his own results for the Mt. Lofty sclerophylls. Patton (1932) listed the number of stomata per sq. mm. in three legumes, *Platylobium obtusangulum* (280), *Bossiaea cinerea* (600), and *Acacia oxycedrus* (120), and of a Myrtaceous plant, *Leptospermum laevigatum* (100) occurring in heath sclerophyll vegetation at Cheltenham in Victoria and drew attention to the considerable degree of variation shown. This variation was also the subject of comment by Wood for South Australian plants. McLuckie and Petrie (1927) gave values

for some sclerophyll and rain forest plants of Mt. Wilson in New South Wales. While the data published is rather limited, it seems clear that for the plastic genus *Eucalyptus*, similar variation in stomatal frequency frequently occurs as was shown by Wood for South Australian *Eucalypts*. The mean value for the four New South Wales *Eucalypts* was 211 and for four members of the Proteaceae it was 154. This may be compared with the Mt. Lofty South Australian figures of 312 for five *Eucalypts* and 145 for eight members of the Proteaceae. The stomatal frequencies for the nine Mt. Wilson sclerophylls were high as compared with the four Rain Forest types (means 215 : 159 respectively) but from the data given it is not possible to say with certainty whether there is any significant difference. Carey (1938) has studied the stomatal frequency in a large number of sclerophylls from sandstone ridges around Sydney. For members of certain families she obtained a picture somewhat similar to that of Wood, e.g., for Proteaceae, the mean value was 162, for Epacridaceae 296, and for Leguminosae, 185.

Preliminary work on sclerophylls of the Swan coastal plain in Western Australia has shown a mean value of 270 for 18 species growing under conditions not markedly different from those of the Mt. Lofty Ranges in South Australia for which Wood recorded a value of 230 ± 19 . Examination of stomatal frequency for individual families shows that there is considerable variation from those of South Australia and from those of the Sydney area, and further work is needed to extend the number of species for comparison purposes.

Detailed determinations on stomatal frequency in sclerophyll vegetation in the Mediterranean region appear to be lacking so that useful comparisons can not be made here.

Turning to the question as to whether high stomatal frequencies are associated with more xerophytic conditions as Salisbury (1927) suggested for Great Britain, Wood (1934) finds no support for this view. Statistical analysis showed that there was no significant difference between stomatal frequencies of South Australian sclerophylls and plants of British woodlands. Although a significant difference was found between stomatal numbers of South Australian sclerophylls and those of the dry patinas of Ceylon (Parkin and Pearson, 1904), Wood doubts the adequacy of Parkin and Pearson's data and concludes that generic and family characters are more important than environment in determining stomatal frequency. The stomatal index for South Australian sclerophylls was also found to be fairly constant (although relatively few species were tested) and to approximate to the mean value given by Salisbury for British woodland plants. Carey (1938) for sclerophylls in the Sydney area concluded that stomatal index was independent of environment. She could find no correlation, however, between stomatal indices of either family or genus. In view of these differences some further comparative investigation of stomatal frequency in sclerophylls from other arid and semi-arid parts of Australia, seems warranted.

Position of the Stomata

In most of the important families in which sclerophylls are represented in New South Wales, Victoria and in South and Western Australia, stomata may occur on both sides of the leaf. An exception is the Epacridaceae in which they are confined to the lower surface. Evenari (1937) in a study of desert plants (not sclerophylls) found more stomata on the upper than on the lower surface and suggested this might be due to the high light intensity. Wood's data (1934) is in direct contrast to this for South Australian arid region plants, for both tomentose succulents (*Kochia*, *Bassia*) and sclerophylls. Wood does, however, suggest that there may be an increase in the percentage of plants possessing stomata on both leaf surfaces when passing from temperate to arid conditions. Thus, in the Mt. Lofty area the percentage with stomata on both sides of the leaf is 79 while at the desert station of Koonamore it is 100.

Summary

The preceding analysis shows that sclerophylls as a class differ in their water relations from mesomorphs, particularly in the dry summer period. The average rate of field transpiration in mg./g./min. is lower than in mesomorphs as is also the rate of movement of the transpiration stream. On the other hand their osmotic pressures are higher than mesomorphs, and also rise with dry summer conditions. Stomatal frequencies and stomatal indices in sclerophylls appear, at least under Australian conditions, to show no correlation with habitat or environment, although there is a suggestion that the percentage of stomates on both surfaces of the leaf increases with increasing aridity.

The Assimilation and Respiration of Sclerophylls

Because of the summer drought conditions to which sclerophylls are normally exposed (due to climate or soil or both) it has been of considerable interest to ascertain whether they enter a period of enforced physiological rest at that time or whether the presence of the xeromorphic modifications they possess allows them to continue active photosynthesis. In the Mediterranean area careful studies have been made in particular of Maquis vegetation which provide answers to the above questions.

Guttenberg (1927) made a qualitative study of assimilation in Mediterranean sclerophylls under climatically favourable and unfavourable conditions. In spring (March-April), when the growth of new leaves was beginning, climatic conditions were very favourable, moisture being adequate and temperature mild, while the stomata were open at their maximum throughout the day, both in sun and shade. The osmotic pressure of leaves (by a plasmolytic method) was found to be approximately 36 atmospheres, while transpiration was relatively high and conditions were suitable for good assimilation. This was reflected by strong starch formation and storage in the leaves. The plants were next studied in summer (August) by which time a condition of extreme drought had de-

veloped. The stomata were found to be only slightly open for a short time in the morning and for a considerably shorter time in the late afternoon while on many days they remained completely closed. The osmotic pressure was found to be much higher than in spring, ranging from 53-69 atmospheres. It was observed also that at the end of the summer period the leaves were more or less denuded of starch and low in sugar. This was taken as evidence that little assimilation occurred during the drought period. The tannin content was also observed to increase in the cells of leaves as the summer drought intensified. With the coming of the wet season the starch content was increased in the leaves for a period of some weeks, but it then began to fall again and by mid-winter had largely disappeared from the palisade cells.

Guttenberg and Buhr (1935) studied quantitatively the assimilation and respiration of Maquis in Corsica in spring and in summer. In spring assimilation was found to be high but in summer it was rather restricted. They concluded that under drought conditions the plants were on the threshold of survival and that a summer rest occurred. The almost complete stoppage of photosynthesis in summer was ascribed to relative lack of water.

Harder *et al.* (1931) worked on desert plants including the sclerophyll *Nerium oleander* (which is also one of the character plants of the Maquis). This shrub was found to occupy dried-out water-courses and even in summer (August) the subsoil remained moist and the stomata stayed open. In the early morning (7 a.m.-8 a.m.) assimilation was greater than respiration showing a positive balance of 3-5mg. CO₂/sq.dm./hr. at 30°C. By 10 o'clock, however, it had fallen to the compensation point where it remained until 4 p.m. after which time assimilation again rose above respiration. Shading of plants resulted in a rise of the rate of assimilation. These results are in general agreement with those of Guttenberg and Buhr. Harder *et al.* investigated respiration only in single cases where it was found to be 0.7 mg./sq.dm./hr. After rain, respiration was found to rise sharply, even under conditions of falling temperature. They believed this could be explained by re-hydration of the protoplasm. In contrast to the findings of Guttenberg (1927) and Guttenberg and Buhr (1935) for Maquis vegetation, Harder *et al.* found no evidence of a drought rest period in the desert plants they studied. Maquis of course has quite a long favourable seasonal period for growth, while desert plants have not and this may prove to be of importance in relation to the absence of a rest period. Killian (1933a) for *Pistacia lentiscus* in Algeria found an assimilation value of 10 mg./sq.dm./hr. in the spring. During summer (June) the curve sank between 11 a.m. and 1 p.m. In the earlier part of the morning reasonable assimilation occurred but by the afternoon it was negligible. Eckardt (1952) reported for Garrigue (modified sclerophyll) plants that during the dry season photosynthesis practically stopped during the afternoon. He

ascribed this to the interaction of a number of factors including relative lack of water, closure of stomata, protoplasmic reactions consequent upon dehydration of colloids and perhaps destruction or change in the chlorophyll pigments.

No quantitative work on photosynthesis or respiration has been done on Australian sclerophylls although Wood (1934) has followed the seasonal variation in carbohydrates. In the absence of experimental work it is not possible to say with certainty whether Australian sclerophylls show greatly reduced assimilation during the dry summer period. Diels (1906) has described vividly the appearance of the dried-out looking vegetation in Western Australia in late summer and suggested that the plants pass largely into a state of suspended animation. It is a matter of common observation that Western Australian species such as *Hibbertia hypericoides*, *Stirlingia latifolia*, *Bossiaea eriocarpa* and *Acacia acuminata* show with increasing dryness a marked yellowing of photosynthetic tissues. Normal green colour returns very rapidly if shoots from these plants are placed in water. The same effect is observed in intact plants after the commencement of the winter rains. It therefore seems possible that photosynthesis may be affected particularly during the latter period of the summer. Studies are now proceeding on Western Australian sclerophylls under field conditions to obtain the necessary quantitative data to clarify this point.

The Metabolism of Sclerophylls

Study of the metabolism of sclerophylls in the Mediterranean region and in semi-arid and temperate Australia has shown some interesting features. Guttenberg (1927) examined starch-sugar-tannin relationships on a qualitative basis in Maquis. He showed that in the spring, starch content was high, the cells of leaves being packed with starch grains. Passing into summer the starch disappeared, and sugar concentration decreased, indicating rapid further breakdown or alteration of products of starch hydrolysis. During this period of increasing drought the tannin content of leaf cells was observed to increase. With the onset of first winter rains, starch grains reappeared but later in deep winter a second reduction in starch content occurred. No determinations appear to have been made to see whether there was any change in sugar content at that time. Wood (1933) in South Australia followed the seasonal variations in carbohydrate content in a broad sclerophyll plant (*Acacia pyrenantha*) and in a needle-leaf sclerophyll (*Hakea ulicina*). Sugar concentrations were found to rise during periods of low temperature and vice versa. The starch concentration was found to be greatest when sugar concentration was low and high sugar was correlated with the period of active growth in each sclerophyll type. This led him to the view that high sugar concentration was related to cellulose wall formation. He noted that there was no difference in sugar/starch relations from other plants or in their seasonal variation.

Wood (1933) seems to have been the only worker so far who has concerned himself with the processes of lignification, cutinization and the changes in tannin content in sclerophylls. Study of these processes is of particular interest under southern Australian conditions where these features are highly developed in sclero-

phylls. Wood observed that the process of lignification started in broad sclerophyll (*Acacia pycnantha*) leaves only when they were reaching maturity after some two months growth (see Table VI) and that lignification proceeded from the base towards the tip of the leaf.

TABLE VI

Process of Lignification in Southern Australian Sclerophylls (after Wood 1933)

	Broad Sclerophyll <i>Acacia pycnantha</i>			Needle-leaved Sclerophyll <i>Hakea ulicina</i>				
	Young	Devel- oping	Mature	2 weeks	6 weeks (Mature)	6 months	18 months	30 months
Lignin (%) ...	0.97	3.2	3.2-3.4	0.65	4.84	5.4	5.5	6.6
Cutin (%) ...	0.4	5.8	7.6-8.2	2.0	9.3	13.8	13.9	13.8
Tannin (%) ...				10.4	8.6	6.0	5.6	...

For needle-leaved sclerophylls, e.g., *Hakea ulicina* which mature in one month but stay functional for three years, there was a continuous increase of lignin with time up to 30 months (see Table VI). As was the case in *Acacia*, the lignification also proceeded upwards from the base of the leaf. The process of cutinisation seemed to be completed by the time the leaf was six months old. Tannin concentration fell with time, and Wood showed that there was a relation here with lignification. Tannin (a product intimately connected with sugar metabolism) is believed to be concerned through its phenolic nucleus with the formation of the lignone complex of lignin. As the presence of thick cellulose walls impregnated with lignin and cutin is such a feature of Australian sclerophylls this is one of the aspects of sclerophyll which requires further study in different parts of the Commonwealth.

The Significance of the Xeromorphic Modifications Found in Sclerophylls

Sclerophylls as a Type of Xerophyte

Any discussion on the significance of xeromorphy in sclerophylls involves consideration of the larger question of xerophytes. In its original sense this word referred to plants which grew in dry areas of the world (Schouw. 1822). Schimper (1903) and Warming (1909) introduced as well physiological and morphological concepts so that a xerophyte came to be regarded as a plant which was exposed to conditions of deficient water supply or which grew in dry places and with which certain morphological features were associated. Maximov (1929) introduced a different physiological concept for xerophytes, characterising them as plants with a high resistance to desiccation. Under both conceptions xerophytes included a variety of plant types:—succulents, perennial semi-succulents, tomentose succulents (saltbushes), non-succulent perennials (herbaceous xerophytes), plants which shed their leaves under very dry conditions, and sclerophylls. It is in this last group, with which we are essentially concerned, that the majority of the morphological modi-

fications described as xeromorphic characters occur. Sclerophylls were defined by Schimper (1903) as plants of the xerophytic bush in sub-tropical regions, where the rain falls in winter. Maximov (1929) enlarged the habitat to include arid regions. As we have seen earlier the main areas of occurrence of sclerophyll vegetation are in the Mediterranean regions, California, Central Chile, the Cape Province of South Africa, and South and Western Australia. It is of considerable interest at this point to examine further the occurrence and distribution of the sclerophyll habit under Australian conditions to see how far it conforms to the above definition of habitat and whether all of it is necessarily xerophytic.

Wood (1924) stated that sclerophylls with their characteristic xeromorphic modification occurred not only in the arid regions of South Australia, but also wherever evaporation was markedly in excess of rainfall as in the sclerophyll forests of the Mt. Lofty Ranges near Adelaide where the rainfall range was from 20 to 40 inches. Osborne (1932) pointed out that for Sydney, near which on the Hawkesbury Sandstone there is a strong development of sclerophyll vegetation, the annual rainfall is 48.2 inches with a mean fall of 2.6 inches during the driest month. The average annual evaporation is 38.45 inches and it exceeds rainfall only during four summer months. The Transeau Ratio (P/E) is approximately 1.3. According to Osborne the Sydney ratio is thus comparable with that of United States cities such as Boston (Mass.), and New Orleans (La.) which come within the area of "southern mesophytic forest" (Livingstone and Shreve, 1921) and yet it has a well developed sclerophyll vegetation. Osborne observed, however, that the plants of the Hawkesbury Sandstone did suffer from periodic drought due to the drying out in summer of the shallow sandy soil in better drained areas. Patton (1932) in discussing the extensive evergreen sclerophyllous vegetation of the sand heaths east of Port Philip Bay in Victoria, stated that while the six summer months from October to March actually received slightly more rain than the six winter months, nevertheless the evaporation during the six summer

months greatly exceeded precipitation. As in the Sydney area the soil factor here is regarded as being more important than climate because of the inability of the soil to retain much water. After a prolonged period of drought, Patton records that the water content of the soil at a depth of 12 inches fell as low as 1.07 per cent.

For the area around Perth where typical sclerophyll vegetation occurs, the average annual rainfall is 34.7 inches and the average annual evaporation is 34.5 inches. The rain falls in winter and for the six summer months of the year evaporation is high and very dry conditions prevail. Passing south towards Albany the climatic conditions approximate more closely to those of Sydney. The vegetation remains markedly sclerophyll in character (becoming modified, however, in the Karri forest) and the country is subject to summer drought. Passing inland the environment rapidly becomes more arid and the degree of sclerophyll more marked. The soil factor is again of great importance because the sandy soils tend to become very dry in summer.

Under all the Australian sclerophyll habitats so far mentioned summer drought is always a possibility and the soils are such that they dry out quickly. Certain areas conform exactly to the picture of Mediterranean climate and other areas fit reasonably with Schimper's conception of habitat of sclerophylls because the effective rain is mainly in the winter months (cf. Patton 1932, page 209). Sclerophylls growing in these areas although always xeromorphic may not necessarily be xerophytic. This has to be determined by experiment.

Not all the sclerophyll vegetation in Australia, however, is confined to the winter rainfall area. On the mainland it extends through New South Wales up to Queensland where the rainfall shows a marked summer maximum and may exceed evaporation during each month of the year. Sclerophylls in this area under our present climate could not come into the category of xerophytes. The same applies to those in Tasmania where Rodway (1914) observed that although the climate of Tasmania was distinctly temperate the larger plants were of decidedly xerophytic (sclerophyll) nature.

This matter will be referred to again when dealing with the origin of sclerophylls.

The Rate of Water Loss from Xerophytic Sclerophylls

Schimper (1903), Benecke-Jost (1924) and others popularized the view that xerophytes, which grew in dry places where water was the most limiting factor, transpired at a lower rate than soft leaved plants in temperate habitats.

Little experimental evidence existed for Schimper's assumption that they did transpire at a low rate but Schimper so profoundly influenced thought at the time that it was many years before his view was seriously questioned. In 1916 the experimental gap first began to be filled when Maximov showed that xerophytic plants in the semi-desert area at Tiflis in Russia transpired at a higher rate than soft leaved

plants from a shaded irrigated garden. Further papers by Maximov, Alexandrov (1922), Huber (1924), and Stocker (1928), appeared to confirm the view that xerophytes as a class transpired faster than mesophytes. In his book, "The Plant in Relation to Water" (1929), Maximov strongly advocated this view and appeared to make exceptions only of the succulents of the cactus type and those plants with continually blocked or deeply sunken stomata. Maquis sclerophylls were considered as belonging to the group which transpired faster than mesophytes under favourable conditions. It is worth noting that none of the xerophytes studied by Maximov near Tiflis or those investigated by other Russian workers such as Vasiliev (1931) appear to be of the sclerophyll type. Seybold (1929) using evergreen plants including at least one typical Maquis plant (*Laurus nobilis*) demonstrated that their transpiration was below that of mesophytic plants and criticized the general conclusions of Maximov. Maximov (1931) replied that these evergreens were not true xerophytes and reiterated his view that true xerophytes of desert regions had a higher transpiration rate than mesophytes. Maximov (1929, 1931) therefore substituted "drought resistance" for the transpiration criterion. Xerophytes were to be distinguished not by reduced transpiration but by the capacity to survive drought and dehydration of tissues with little or no injury. The revised Schimper definition according to Maximov (1931) should read:—"Xerophytes are plants of dry habitats which are able to decrease the transpiration rate to a minimum when under conditions of water deficiency". So far as can be ascertained, however, Maximov has given no experimental evidence on the march of transpiration of a xerophyte when passing from moist season to drought, to indicate when the reduction of transpiration would occur. Moreover it almost appears that sclerophylls are excluded from his concept of "true xerophytes", since they are not restricted by any means to desert areas. With the passage of years, intensive work on transpiration, particularly in areas subject to summer drought has led to accumulation of a considerable body of data, the relevant parts of which in the case of sclerophylls have been reviewed earlier in this paper. Some disagreement with Maximov's viewpoint has emerged.

Henrici in South Africa (1937, 1940a, 1940b) pointed out that the Karroo types of xerophyte (including large Karroo sclerophylls) were different from Maximov's Tiflis type, because only rarely did they transpire highly even in the presence of adequate water. They not only restricted their water loss with declining water supply of the soil, but also restricted transpiration even with adequate water during the hot part of the day. She indicated that Maximov's (1929) findings on the "high transpiration of xerophytes" applied for Karroo bushes only when the soil was about half saturated, a condition which was seldom met with on the veld. While she agreed that (under specific conditions) plants in drier regions undoubtedly had the ability to transpire freely, it was more important to know what the plants did under the adverse conditions which probably prevailed for a great part of their lifetime.

Oppenheimer (1951) in reviewing work on water relations of plants in the Middle East, claimed that xerophytes with xeromorphic structures had a lower average transpiration rate than mesomorphs provided that total average water use was expressed in terms of fresh weight of plant or per unit of soil area permeated by the roots. While agreeing that Maximov was probably right in demonstrating that certain xerophytes have very high transpiration intensities when well supplied with soil moisture, he differed from that author in contending that xerophytes (including sclerophylls) lived normally under conditions of low water supply during the summer in the Middle East and did reduce their water loss before a condition of extreme water deficiency supervened. This view is essentially similar to that of Henriel. Oppenheimer claimed further that even if the transpiration rate of xerophytes did at times exceed that of a mesophyte the overall loss was still less because of greatly reduced leaf area. Here he opposes the views of Stoeker (1923) and of Thoday (1931) that the reduction in size of the sclerophyll leaf has been accompanied by a more than compensating increase in the total leaf area because of the total number of leaves present. In this connection Patton (1932) had earlier criticized Thoday's view, as his study of Victoria heath sclerophyll vegetation had provided evidence to show that the total leaf area did not compensate for the generally small size of the leaves. The author's observations on Victorian and Western Australian sclerophylls support the contentions of Oppenheimer and of Patton.

Patton (1932) also held that the sclerophyllous heath vegetation of the Cheltenham area in Victoria needed to economise water during the regularly recurring drought period. He did not cite any transpiration experiments but stated that the restriction of transpiration was accomplished not only by the reduced size of leaves, but also by the reduction of total leaf area.

Wood (1933, 1934, 1939) believed that his transpiration results for Australian sclerophylls, taken together with results of overseas workers on xerophytes, mesophytes and shade plants in Swedish Lapland, Germany, the Tyrol, the Mediterranean region and Arizona, disposed equally of the older view that xerophytes had a reduced transpiration rate compared with other plants and of Maximov's contention that they had an increased one. Plants from the diverse habitats mentioned were stated to have a mean transpiration per unit area of 1500-2000 mg./sq.dm./hr. (25-33 mg./sq.dm./min.) A study of his results (see Table II) would not appear to bear out this statement for South Australian sclerophylls. Thus his average value for the Dilkeria, Curnamona, Koonamore and Mt. Lofty areas is 5.4 mg./sq.dm./min. The average rate for the Dilkeria and Curnamona areas is 1.8 mg./sq.dm./min. Only in the Mt. Lofty area is the average rate somewhat high (16.94 mg./sq.dm./min. with a range from 7.0-26.6 mg./sq.dm./min. As mentioned earlier these results are well above those obtained by the author for similar sclerophylls in comparable areas in Victoria and Western Australia under field conditions in summer. In any case even the Mt.

Lofty results scarcely come within the range Wood mentions for other areas. Study of the results of workers elsewhere on sclerophylls (see Table III) show their figures to be well below the 25-33 mg./sq.dm./min. Only in the case of mesophytic plants growing under comparable conditions (including Wood's own result for the mesomorph *Senecio magnificus* at Curnamona) are there clearly indicated higher rates of transpiration. It may be noted that the rate for *Senecio magnificus* approximates very closely to that given by Maximov (1929) for mesophytic sun plants such as *Erodium ciconium* and *Hirschfeldia adpressa* at Tiflis. It therefore appears to the author that southern Australian sclerophylls, growing in areas subject to summer drought (due to either climate or soil or both) have as a class lower average rates of transpiration than mesomorphs growing under comparable conditions in summer and that they reduce their water loss before extreme water deficiency conditions develop. The different physiological groupings within the sclerophyll class under Southern Australian conditions will not be considered here, nor the sclerophyll types which, as has been mentioned, grow in areas in Australia where the climatic and soil conditions indicate that they are not xerophytes.

The Function of Xeromorphic Modifications in Sclerophylls

Schimper (1903) believed that the function of xeromorphic characters was to reduce water loss. Maximov (1929, 1931) when he found that the water loss of xerophytes with xeromorphic modifications (growing in Tiflis) was greater than that of mesophytes there, concluded that these structures were only of protective value when the plant was wilting. Bennett-Clark (1945) accepted Maximov's conclusion that the function of xeromorphic modifications was not to hinder water loss. As their occurrence seemed to him scarcely accidental, however, he suggested that they might serve to facilitate photosynthesis acting as mechanisms which protected the stomata and enabled them to keep open longer during drought conditions. Thus they would actually favour increase of transpiration, and of course, the diffusion capacity of the epidermis for carbon dioxide. He suggested that they operated by maintaining a relatively moister atmosphere around the stomata and neighbouring epidermal and mesophyll cells than would otherwise be found, thus inhibiting closure and maintaining high diffusion capacity. Bennett-Clark argued from this that leaves deprived of say, hairy coverings, should have less widely open stomata and so should transpire less. He tested this experimentally but while there was some suggestion of reduction in shaved leaves under very dry conditions he could not show the results to be significantly different from water loss of unshaved leaves. In other experiments using leaves of rolled plants which had been forcibly unrolled, Bennett-Clark found no significant difference between their transpiration rates when both were exposed to an atmosphere of about 40 per cent. relative humidity. If leaf

inrolling had physiological significance in the Schimper sense the transpiration in the rolled leaves should have been lower. Bennett-Clark suggested as explanation that the stomata were protected or prevented from shutting by being enclosed in the rolled leaf. These experiments were done under laboratory conditions and would need testing under field conditions. It may be noted, however, that there are already available certain results for sclerophylls and also tomentose succulents (saltbushes) which bear somewhat unfavourably on the theory. Thus Guttenberg and Buhr (1934) have shown in the case of Maquis that considerable reduction in rate of photosynthesis occurs with advancing summer and that plants enter upon a resting period. Eckardt (1952) has also shown for Garrigue vegetation that both photosynthesis and transpiration decrease during the dry season and that depression of transpiration in the afternoon may occur independently of any change in photosynthetic activity. Wood (1923, 1932), has also demonstrated very effectively for South Australian tomentose succulents (saltbushes) growing in semi-arid areas, that as compared with mesophytes, there is a strikingly low transpiration rate and also a lower photosynthetic rate. In the light of these results for two types of xeromorphs and also of other data presented on control of transpiration in sclerophylls it seems somewhat unlikely they function in the manner Bennett-Clark suggested.

Oppenheimer (1951) in discussing the structural peculiarities of sclerophyllous evergreens indicated that the studies of such early workers as Guttenberg (1907) suggested that thick epidermal walls, cutinization and sunken stomata were effective means of protection against water loss in times of emergency. Having noted that later authors felt unable to corroborate these conclusions by experimental studies, he went on to emphasize that his experience with plants growing under natural conditions in Palestine led him to support the classical interpretation. He instanced some of his work (1947) on sclerophyllous species of the Maquis where a considerable transpiration was suddenly reduced to zero by stomatal regulation. As he pointed out this can only be understood by the assumption that cuticular transpiration was not taking place or was negligible and that stomatal regulation was highly effective.

Henrici (1940a) examined the question of stomatal opening in relation to transpiration of large sclerophyllous bushes of the Karroo. For these plants the low daily water losses in times of drought was found to be due to stomatal control. The stomata either remained closed all day or they closed after a short period of rapid transpiration, so that transpiration values scarcely exceeded those of cuticular transpiration for the whole day.

From studies on Western Australian sclerophylls the author has concluded that stomatal regulation plays a large part in controlling water loss, although other internally operating factors (osmotic and protoplasmic) are believed to be concerned.

The evidence for control of water loss from sclerophylls in the three areas mentioned seems to point to some differences from the views of Maximov (1931) for xeromorphic xerophytes. Giving a hypothetical case of a xerophyte exposed to increasing dryness, Maximov states that "when the plant is wilting, when its stomata are closed and when the loss of water takes place only through the cuticle, then all these anatomical peculiarities manifest their protecting properties".

The experimental evidence for sclerophylls (and also for several other non-sclerophyllous xerophytes (cf. Henrici, 1940b; Oppenheimer 1951) is that average water loss is lower and that stomatal control (with the assistance of the xeromorphic features) may occur long before the plant is at the wilting stage.

Theories of Origin of Xeromorphic Modifications

Turgor Theory and the Experimental Induction of Xeromorphy (Xeroplasty)

Kohl (1886) believed that the development of "protective means" as the modifications were then described, was due to strong transpiration. He based this on the experimental induction of xeromorphic features (such as thick cuticle, thickening of epidermal walls, etc.) in plants growing in dry air. Schimper (1903) by contrast concluded that it was the amount of transpiration relative to water supply, rather than the absolute transpiration which was responsible. Zaleski (1904) confirmed Kohl's observations noting that leaves of plants growing in dry open habitats were more xeromorphic than those of plants growing in woodland shade. Rippel (1919), Alexandrov (1922), Tumanov (1927), Maximov (1916, 1929), and others confirmed experimentally that some xeromorphic characters could be induced by growing plants under dry conditions. Maximov (1929) stated that the xeromorphic modifications in the xerophytes he worked with were induced by solar radiation and water deficit in the leaves. Normal development of cells was considered to be prevented owing to lack of water in the embryonic tissues and consequently cells remained smaller and developed thicker walls. Other structural peculiarities followed from this.

Walter (1926) explained on a basis of osmotic pressure effects how reduced turgor would result in decreased size of cells and the development of more numerous stomata. Ashby (1933) produced supporting evidence by showing that increase of xeromorphy was correlated with reduced turgor in upper leaves.

It was pointed out by Thoday (1933), that as some plants (in particular many xerophytes) were relatively non-plastic and their xeromorphic features were hereditary, that Maximov's use of the term "xeromorphic" in relation to the above was confusing. Thoday therefore suggested "xeroplastic" as a more appropriate word to cover those conditions where features of form and structure suggestive of xerophytes or xeromorphy, could be shown by experiment to be produced or intensified by desiccating conditions. He stated that similar features shown

by a desert plant or sclerophyll plant in less arid areas, could not be assumed to be xeroplastic until experiments with that species had demonstrated them to be so. Daubenmire (1947) supported this view indicating that xeroplastic features were induced by drought and so only occurred under dry conditions, but because of genetic fixity xeromorphic features were inherited under any environmental conditions. According to Thoday (1931) the development of the microphyllous sclerophyll habit (ericoid, pinoid leaves) may be related to reduction of internal resistance so that no part of the mesophyll is more than a short distance from the main channels of supply. The experimental evidence suggesting this was first put forward by Yapp (1912). Martin (1943) has also pointed out that the smallness of the leaf blade renders it less likely to over-heat under semi-arid or arid conditions.

Xeromorphy due to Altered Metabolic Flux due to Mutations in Protoplasmic Constitution

Wood (1933) very aptly pointed out that the work on induced xeromorphy described above was developed in relation to upper and lower leaves of annual or mesophytic plants and by an *ad hoc* argument transferred to xeromorphs generally. For southern Australian plants growing in sclerophyll forests he considered that Maximov's theory of origin of xeromorphic characters could not apply, as leaves of such plants were not subjected to high tension of meteorological factors. Growth according to Wood "commences early and the foliar organs attain mature size and structure in the great majority of cases during the wet winter months. During these months the ground in the sclerophyll forests is saturated with water, the rainfall exceeds the evaporation to a considerable degree, the mean relative humidity is high and the mean temperature low." He could find no lack of turgor in cells of typical sclerophylls, e.g., *Hakea ulicina* and *Acacia pycnantha*, during the period of development, such as Yapp (1929) found in *Spiraea*. Wood further pointed out, as we have noted earlier, that the sclerophyll type of vegetation is not confined to the Southern regions with a Mediterranean climate, but occurs also in eastern New South Wales and Queensland, where the rainfall shows a summer maximum and where rainfall exceeds evaporation during each month of the year. He therefore concluded that the outstanding characteristics of Australian xeromorphic (sclerophyll) plants were not determined by water deficits. From biochemical studies of sclerophylls he concluded that they were, however, determined by fundamental changes in the metabolic flux of carbohydrates. These changes he believed were probably due to a deep-seated mutation of protoplasmic constitution.

While agreeing that lignification and cutinization characteristic of sclerophylls may proceed from an altered metabolic flux, the author nevertheless is of the opinion that the generalization made regarding the absence of water deficits in Australian sclerophylls is rather too sweeping.

Although detailed information is still lacking there is reason to believe that in many sclerophylls, embryonic leaves are developing at a time of water stress and this as Nordhausen (1903) (*cf.* Maximov (Yapp) 1929) has indicated may pre-determine stomatal size and number, thickness of walls etc. A study of leaf ontogeny therefore seems necessary before it can be stated categorically for all existing Australian sclerophyll vegetation that the water factor is not concerned in the development of the xeromorphic modifications characterizing sclerophylls. The habitat of many Western Australian sclerophylls, the conditions obtaining during their vegetative growth phase and the transpiration results in summer drought also suggest that climatic stress must still be considered in relation to the origin of xeromorphy.

Xeromorphy due to mineral nutrition

In the course of work on nitrogen nutrition in plants, Mothes (1932) discovered that it was possible to induce certain xeromorphic features in plants by nitrogen deficiency. He considered that low nitrogen like a water deficit, induced high osmotic pressures which in turn brought about xeromorphic features. Marthaler (1939) continued this line of investigation and concluded from his studies of high moor plants in Germany, that nitrogen had no specific effect in relation to xeromorphy, although relative lack of the element did induce some xeromorphic characters. Wood (1934) put forward the view that the deficiency in mineral bases other than alumina and iron in the areas where Australian sclerophyll vegetation grows, might be responsible for their xeromorphy. Beadle (1953) compared the development of plants on the relatively fertile Wianamatta Shales and Narrabeen Shales (which are rich in phosphate) with the stunted, highly xeromorphic sclerophyll vegetation characteristic of the Triassic Hawkesbury Sandstone. Pot culture experiments with fertilizers suggested to him that the degree of xeromorphy of the leaves of some plants was determined by the supply of both phosphate and nitrate.

Specht (1952) working in South Australia on the sclerophyll vegetation of the light land area of the ninety mile plain has taken a more conservative view as to the influence of nutrients in relation to xeromorphy.

From the evidence so far to hand it seems that the effect of lacks in mineral nutrition in inducing xeromorphy must be regarded as a valuable line of enquiry, but it appears necessary to determine whether we are here dealing with a xeroplastic effect or really getting at the origin of xeromorphy. It seems likely that more progress in determining this might be made by the comparison of selected sclerophylls grown from seed in manured and non-manured plots under natural conditions. So far it should be noted that the more striking xeromorphic features of sclerophylls, namely sunken stomata and pits and great development of cuticle and woody tissue (lignification) have not been produced or suppressed by experimental treatments.

Xeromorphy due to intense light

It has been shown by many workers (Bergen 1904, Penfound 1931, Turrell 1944, Shields 1951) that intense light can induce a certain degree of xeromorphy in plants. The criteria used in assessing this increased xeromorphy were greater thickness of leaf and of palisade tissue. As in the case of mineral nutrition the criticism may be made here that the effects produced are possibly only of a xeroplastic nature. No experimental evidence on the formative effect of light under field conditions appears so far to be available for sclerophylls and firm conclusions must await new experiments in this direction.

Summarised Conclusions

The examination of the physiology of sclerophylls growing in areas of summer drought has shown that as a class they possess certain well defined features which mark them off from some other xerophytes, and from mesophytes. In their water relations they show a capacity to restrict transpiration during the summer so that on the average they lose water at a lower rate than mesophytes and xerophytes of the type studied by Maximov. Restriction of transpiration is achieved partly by stomatal closure (when the characteristic xeromorphic modifications can exercise their effect), partly by the opera-

tion of a protoplasmic factor arising out of altered osmotic pressure which increases with advancing summer, and partly by reduction in overall leaf area particularly in ericoid and needle-leaf sclerophylls. In contrast to the types of xerophyte studied by Maximov the restriction of transpiration in Karroo sclerophylls, Maquis and Australian types of sclerophyll may occur well before conditions of extreme water deficiency supervene. Photosynthesis also shows progressive reduction with advancing dry season and in contrast to some semi-desert xerophytes, Maquis sclerophylls appear to pass into a period of greatly reduced physiological activity. Their metabolism shows many points of difference from that of other plants, the emphasis in the broad leaf and needle leaf types being upon lignification and eutinisisation which takes place when the leaf is reaching maturity. The xeromorphic modifications stem from the above alterations in metabolism, but their origin remains obscure. Modifications so far induced experimentally appear to be xeroplastic in nature and further research is required to determine to what extent inadequate supplies of water, lack of essential elements at significant phases of growth, or high solar radiation, condition true xeromorphy in sclerophylls.

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6—Devonian and Carboniferous Spiriferids from the North-West Basin, Western Australia *

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The spiriferid fauna from the newly discovered Devonian and Carboniferous rocks of the North-West Basin of Western Australia is described. One new genus and species, *Austrospirifer variabilis*, and four new species, *Cyrtospirifer minilyaensis*, *C. australis*, *C. gneudnaensis* and *C. brevicardinis* are described from the Upper Devonian, and three new species, *Spirifer fluctuosus*, *Punctospirifer plicatosulcatus*, and *Syringothyris spissus* from the Lower Carboniferous. The relative taxonomic value of the various morphological features in tracing phylogenetic lineages within the articulate brachiopods is critically examined. Special consideration is given to those features which affect the spiriferids, and it is concluded that the Spiriferidae constitute a single phylogenetic lineage.

Introduction

Sediments of Palaeozoic age were recorded from the North-West geographic division of Western Australia as early as 1848. Little was known of these rocks until 1907, when A. Gibb Maitland carried out a geological reconnaissance of the area. Further contributions were made by F. G. Clapp, H. G. Raggatt, and C. Teichert, so that by 1947, Teichert was able to present a fairly comprehensive account of the structure and stratigraphical succession. The North-West Basin was stated to cover an area of 40,000 square miles along the coast of the Indian Ocean, between 22° and 28°S. Rocks of Permian, Jurassic, Cretaceous and Tertiary age, with a maximum thickness of 13,000 feet, were known. They were recognized as forming a half basin, open to the sea on the western side, and bordered by the pre-Cambrian crystalline complex to the east. A regional westerly dip and a thickening of the sediments to the north were recorded.

In 1949 a field party of the Commonwealth Bureau of Mineral Resources approached the eastern margin of the Basin with the object of mapping what were believed to be the basal beds of the Permian System. In the vicinity

of Williambury Station, situated at about 24° S. and 110 miles inland from the coast, a thick series of Devonian and Carboniferous marine sediments was discovered. It was from these rocks that the fossil material which forms the basis of the present paper was collected.

The author's thanks are due to the Director of the Commonwealth Bureau of Mineral Resources for permission to describe the material. The serial sectioning apparatus was built by the technical staff of the Department of Geology, University of Melbourne. I wish to express my gratitude to Dr. C. Teichert for advice and criticism during every phase of the work, and to Prof. R. T. Prider for critically reading the manuscript.

All type material is stored with the Bureau of Mineral Resources, Geology and Geophysics, Canberra, Australia. The type numbers given in the text are those of the Bureau of Mineral Resources, and all locality numbers used refer to the Bureau of Mineral Resources' field localities.

Stratigraphy

Nannyarra Greywacke.—This is the basal Formation of the Devonian which rests on the underlying Pre-Cambrian crystalline complex. It is unfossiliferous and of variable lithology.

Gneudna Limestone.—This Formation, which lies conformably on the Nannyarra Greywacke, consists of a fairly uniform series of limestones with a thickness of 2,500 feet. Spiriferids first appear 600 feet above the base of the Formation, and are present through a thickness of 870 feet. New species of *Cyrtospirifer* (see Table I) fix the age of this fossiliferous horizon as late Frasnian. It has been shown (Crickmay 1952) that this genus is confined to the Chemung stage of the North American successions and is distinct from the younger *Cyrtiopsis* fauna of the Famennian. The presence of over 4,000 feet of sandstone between the *Cyrtospirifer* beds and the lower Mississippian Moogooree Limestone is in accordance with this age determination. The associated fauna of the Gneudna Limestone includes corals, stromatoporoids, nautiloids, *Tentaculites*, *Atrypa*, *Hypothyridina*, and *Productella*.

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TABLE I

Field No.	Distribution of Species	Feet above base of Section 1380
206	<i>Austrospirifer variabilis</i>	1229
200		1200
29		1180
20		1170
197		1140
195		1130
194	<i>Cyrtospirifer minilyaensis</i>	1120
193		1100
189		1000
17		975
184		965
183		960
182	<i>Cyrtospirifer australis</i>	950
181		945
180	<i>Cyrtospirifer gneudnaensis</i>	935
178		920
177		600
151		

Stratigraphical distribution of the Upper Devonian spiriferids from the Gneudna Limestone of the North-West Basin, Western Australia. Stratigraphic horizons are given with respect to the base of the Gneudna Limestone.

Munabia Sandstone.—This Formation overlies the Gneudna Limestone with conformity. It consists of fine-grained current-bedded sandstones with some conglomeratic horizons towards the top. The thickness has been estimated at 2,850 feet. No fossils have been found, but from a consideration of the age of the underlying and overlying Formations, a Famennian age for the Munabia Sandstone seems probable.

Moogooree Limestone.—This Formation overlies the Munabia Sandstone with conformity. It is a rather uniform series of limestones and dolomitic limestones with a thickness of 900 feet. Occasional fossiliferous bands are found in the upper half of the Formation. One such band contains numerous specimens described below as new species of *Syringothyris*, *Punctospirifer* and *Spirifer*. The band has a thickness of 5 feet, and is situated 400 feet above the base of the Formation. The fossils are generally silicified, and were freed by dissolving the matrix in hydrochloric acid. The associated fauna includes productids and a species of *Rhipidomella*.

Syringothyris is the only genus recognized which has a moderately restricted stratigraphical range. This genus has been reported from the Permian of India, Spitzbergen and Australia, but in each of these cases the identifications were made on unsatisfactorily preserved material. The undoubted range of the genus is from Conewango to Keokuk times. *Syringothyris spissus*, the Western Australian species of *Syringothyris*, is not a typical representative of the genus, but nevertheless it seems probable that the rocks from which it came are of late Devonian (Conewango) or early Mississippian (pre-Warsaw) age.

Williambury Sandstone.—This Formation rests conformably on the Moogooree Limestone, but the lithological change is sharp. Conglomerates are characteristic of the lower part, whereas the upper parts of the Formation consist of fine-grained sandstones. The thickness of the Williambury Sandstone is somewhere in the vicinity of 2,000 feet. The nature of the stratigraphic association between the Williambury Sandstone and the overlying Permian rocks is obscure, since in all observed areas they are in contact along Tertiary fault lines. Carboniferous and Permian rocks in their respective fault blocks have the same general attitude and dip, so that no large scale diastrophism can be expected between the two Periods. The basal beds of the Permian System (Lyons Group) are almost certainly of Sakmarian age. Thus although no fossils have been found in the Williambury Sandstone, it appears from the associated rocks that this Formation is of middle or upper Carboniferous age.

Terminology and Morphology

In order to avoid ambiguity and unnecessary repetition, the precise meanings applied to several frequently occurring terms are given in the following section. Brief explanations are added where new interpretations of function or nature of morphological features have been made.

Growth Stages.—In separating specimens of two closely allied species, considerable difficulty is often found in determining whether variation is interspecific or merely a function of age of the individual specimens. It is frequently impossible to decide exactly what growth stage an

individual has reached. Since such features as the general shell shape vary with age, within wide limits, this inability to determine the age of an individual presents serious difficulties to the taxonomist. In a complex series of closely allied species, such as is found in the Upper Devonian of Western Australia, confusion may easily arise as the result of grouping mature representatives of a phylogenetically primitive stock with immature representatives of a more highly evolved group.

From the preceding remarks, it may be readily seen that the recognition of morphological features which give some indication of the age of an individual are of primary importance. Such criteria do exist, and although absolute accuracy is never attained, careful consideration of all the available data may result in a reasonable estimation of the growth stage reached by a specimen, especially when the number of specimens considered is large. The following are the growth stage terms used in the present study, with indications as to their delimitation. The *nepionic growth stage* represents the period of growth of the true shell immediately succeeding the embryonic shell or protegulum, but before undoubted specific characters become evident. Practically all spiriferids are more brachythyrid in the nepionic stage than in the neanic and ephebic stages, although they may again attain an equally brachythyrid outline in the gerontic stage. Surface macro-ornamentation is not generally well developed. During the *neanic growth stage*, all the features which characterise the adult are progressively developed. Spiriferid shells are usually megathyrid in the early neanic growth stages and may have the relative length of the hinge line reduced as maturity is approached. Features of the rostral area are never obscured by the secretion of an apical callosity in the neanic growth stage. The *ephebic growth stage* is initiated when the development of all adult specific features is completed. Spiriferids are generally more inflated at maturity than in earlier growth stages, and the area of maximum shell secretion often changes from the cardinal extremities to the anterior margin. The variations in the *gerontic growth stage* may be striking and complex. Shell secretion often results in obesity and thick shells. The rostral callosity is frequently developed to the stage where it completely obscures the finer internal structures of the rostral area. Shells which were megathyrid at maturity may become subquadrate and even brachythyrid in outline. Closely spaced lamellose growth lines are sometimes developed.

Hinge Denticles.—These are the minute elevated inward crenulations in the anterior margin of the palintrope of many brachiopods (Plate 7—6, 8, 11, 13). They are confined to the pedicle valve, and articulate with shallow *denticle pits* (Plate 8—6) in the brachial valve. *Denticle grooves* (Plate 7—8) are shallow grooves on the surface of the ventral palintrope, irregularly spaced, and orientated approximately at right angles to the hinge line; they trace the ontogeny of the hinge line crenulations.

In his study of *Syringothyris*, North (1920) noticed that well-preserved specimens of this genus possessed a palintrope which was clearly

divided into three triangular portions. The two lateral portions showed growth lines parallel to the hinge line and were similar in shell structure namely in the possession of punctae, to the remainder of the shell. The central portion, which was bisected by the delthyrium, was impunctate, and in addition to horizontal growth lines showed irregularly-spaced grooves at right angles to the hinge line. These grooves were continuous with a series of minute denticles along the hinge line, the denticles articulating with shallow sockets in the brachial valve. There can be little doubt that the function of the denticles was to steady the valves, especially in forms with extended hinge lines and proportionally short teeth.

In discussing the origin of the denticles, Young (1884) suggested that they were due to the presence in the hinge line of the living animal of fibres of aragonite, which, "being harder than the ordinary calcite of the shell went to the formation of the row of denticles." He concluded that the vertical grooves on the palintrope were the result of different degrees of resistance offered by calcite and aragonite to subsequent alteration, since aragonite, though harder than calcite, is more soluble than that mineral. The corresponding pits of the brachial valve were supposed to have been formed solely by the friction of the harder projecting aragonite denticles of the pedicle valve.

The structure of these denticles and corresponding pits is shown in detail by many of the specimens of *Spirifer fluctuosus*, n.sp. from the Carboniferous of the North-West Basin, Western Australia. Minute inward folds occur at irregular intervals along the anterior margin of the palintrope. These crenulations are slightly elevated and sharply pointed, forming denticles. The narrow grooves on the surface of the palintrope, directed at right angles to the hinge line, trace the path of these hinge line crenulations through the ontogeny of the specimen. Bifurcation and anastomosis of the denticle grooves is not rare.

Techniques

Most of the Devonian spiriferids described in the present work were completely freed from matrix on their external surfaces during the weathering processes which released them from the parent rock. They were however filled with matrix, so that serial sections were necessary to reveal the internal structures.

The sectioning apparatus used consists of a horizontal mounting plate supported on a rigid tripod. The height of the attachment plate above the plane of the tripod legs may be adjusted by a micrometer screw graduated in intervals of 0.01 mm. Fossils are attached to the plate with sealing wax, and parallel serial sections ground by moving the tripod on a sheet of plate glass, so that the fossil moves with a circular motion over an abrasive disc held rigidly in the centre of the glass sheet. Section intervals of 1 mm. were found satisfactory in most specimens, although it was sometimes necessary to reduce the section interval to 0.5 mm. to gain a clear indication of some of the finer structures of the rostral area.

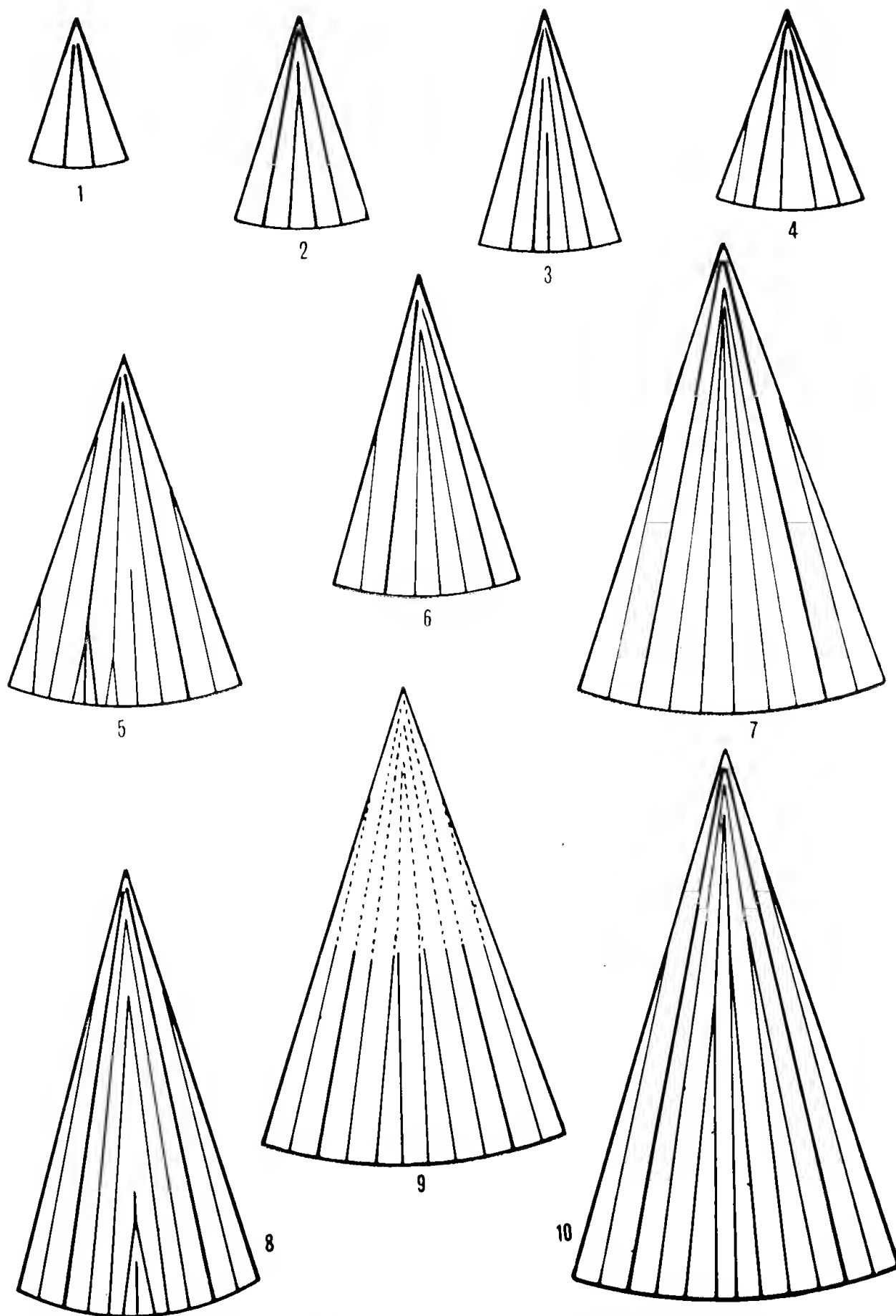


Fig. 1.—Scale diagrams of sinuaplications (length x 2, width x 4).
 1-4—*Austrospirifer variabilis* Glenister, n.gen., n.sp. 1, hypotype No. 449; 2, hypotype No. 450; 3, holotype No. 426; 4, hypotype No. 453.
 5-10—*Cyrtospirifer gneudnaensis* Glenister, n.sp. 5, hypotype No. 466; 6, hypotype No. 467; 7, hypotype No. 468; 8, hypotype No. 469; 9, holotype No. 428; 10, hypotype No. 471.

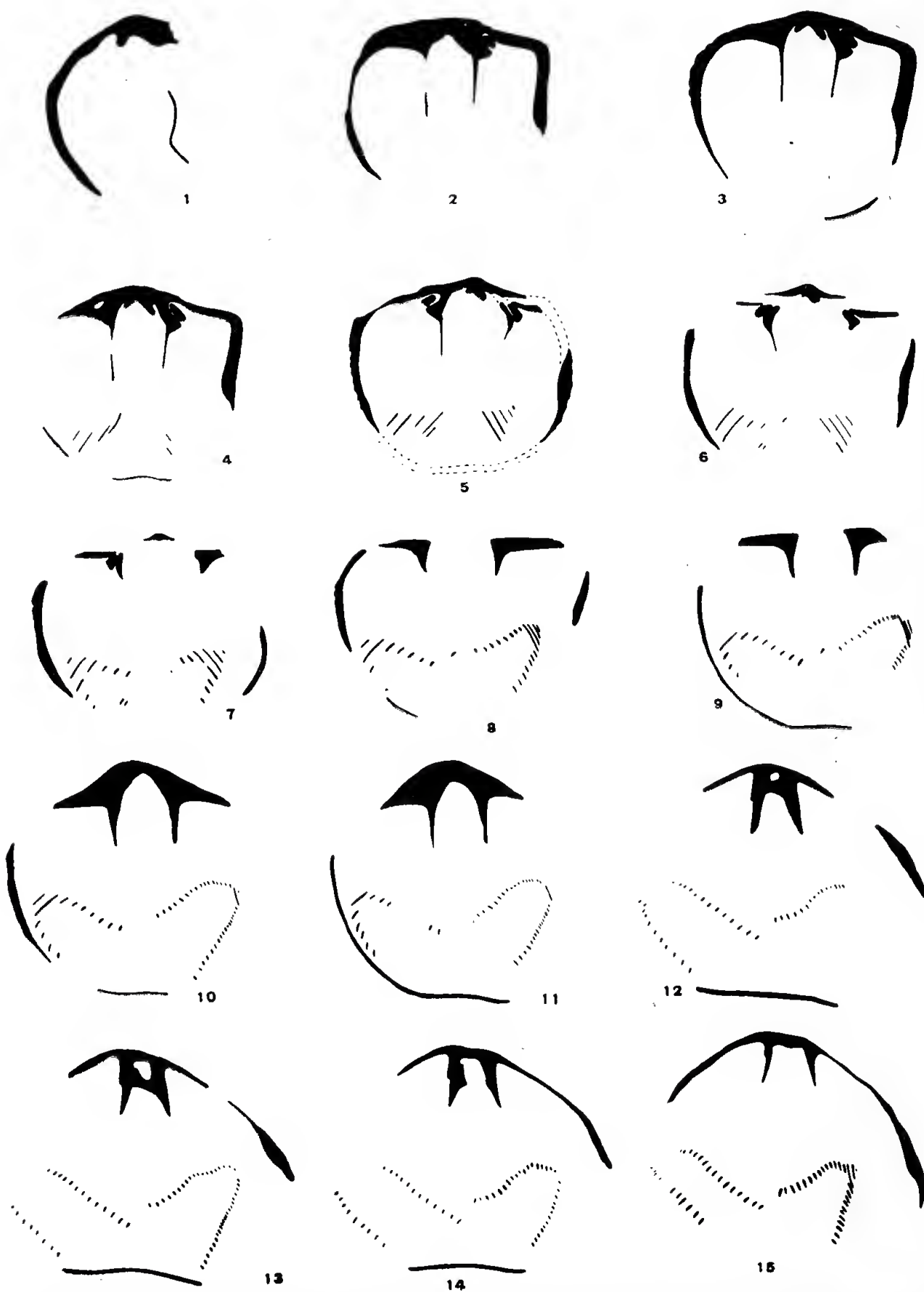


Fig. 2.—1-15—*Cyrtospirifer australis* Glenister, n.sp. Serial sections taken at 1 mm. intervals on paratype No. 440 parallel to the plane of commissure, x 1.2 (approx.). The figures were drawn onto photographic positives, made by using the celluloid serial sections as photographic negatives.

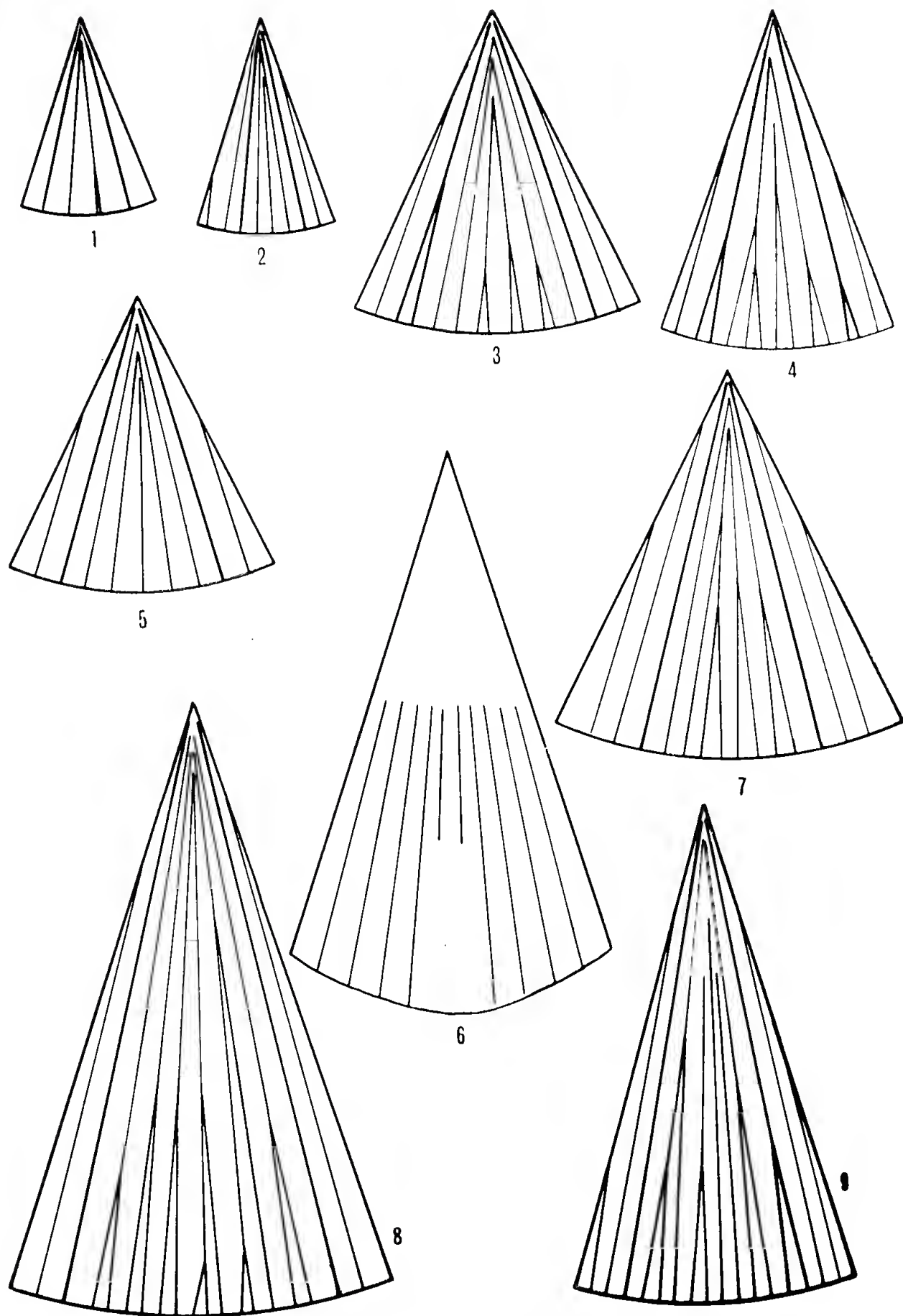


Fig. 3.—Scale diagrams of sinal plications (length x 2, width x 4).
 1-5—*Cyrtospirifer minilyaensis* Glenister, n.sp. 1. hypotype No. 457; 2, hypotype No. 458; 3, hypotype No. 459; 4, hypotype No. 460; 5, holotype No. 477.
 6.—*Cyrtospirifer brevicardinis* Glenister, n.sp. Holotype No. 429.
 7-9—*Cyrtospirifer australis* Glenister, n.sp. 7. hypotype No. 461; 8, holotype No. 427; 9, hypotype No. 463.

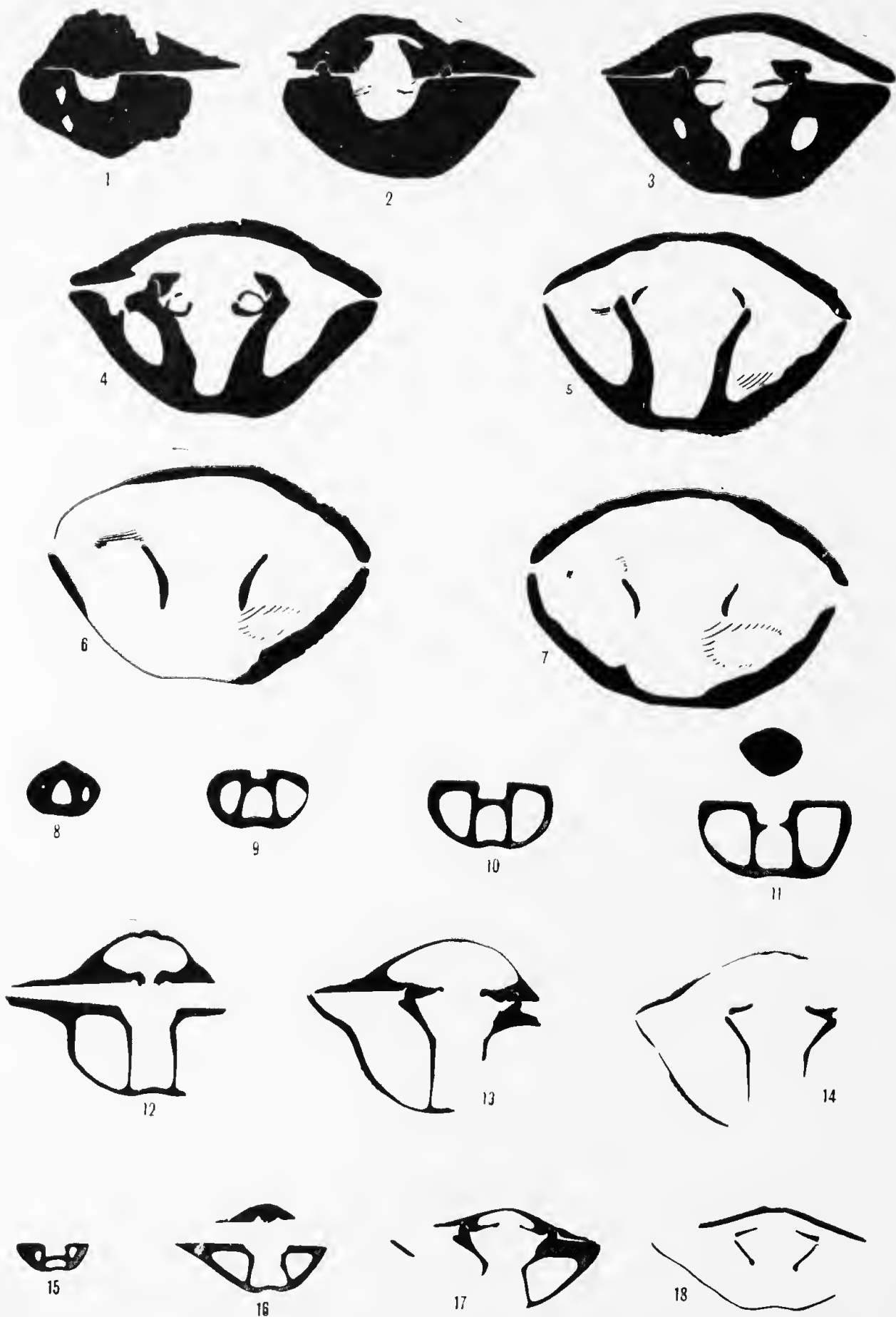
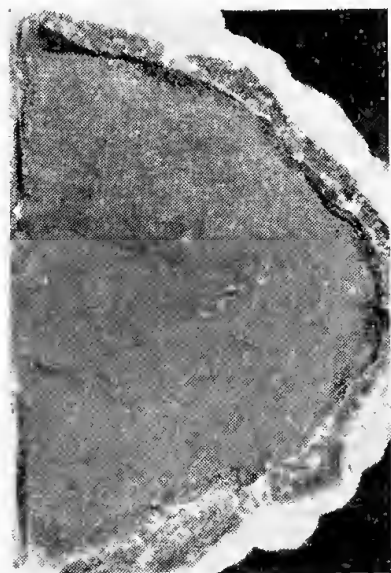
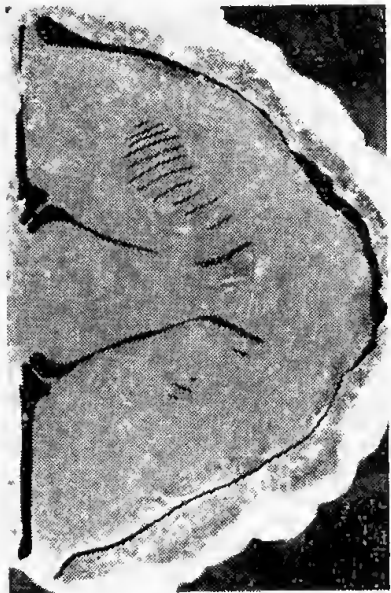


Fig. 4.—Serial sections taken at 1 mm. intervals at right angles to the plane of commissure, $\times 1.7$ (approx.). The figures were drawn onto photographic positives, made by using the celluloid serial sections as photographic negatives.

1-14—*Cyrtospirifer australis* Glenister, n.sp. 1-7, paratype No. 441; 8-14, paratype No. 439.
15-18—*Cyrtospirifer gneudnaensis* Glenister, n.sp. Paratype No. 442.



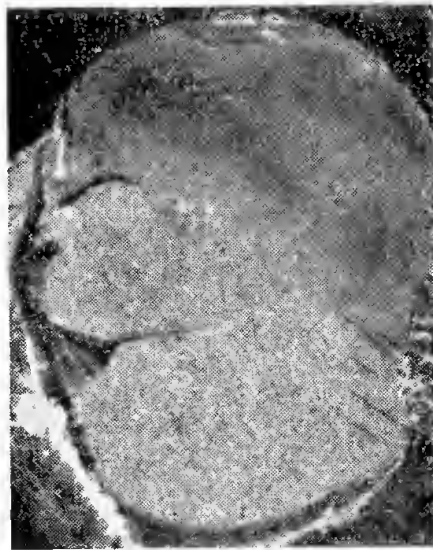
1



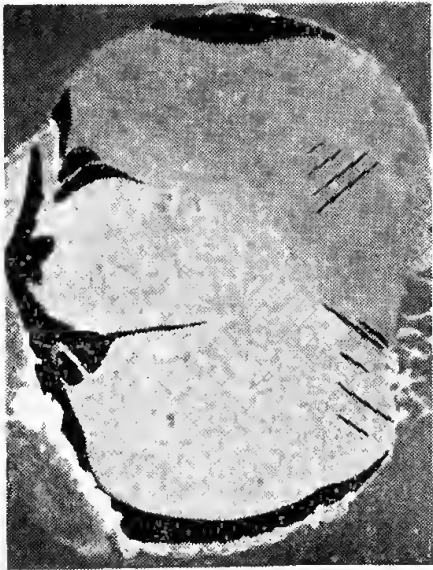
2



3



4



5



6



7



8



9

PLATE 1

Successive stages in the construction of serial section diagrams. All figures x 2.
 1-3—*Cyrtospirifer minilgaensis* Glenister, n.sp. Paratype No. 438.
 4-9—*Cyrtospirifer australis* Glenister, n.sp. 4-6, paratype No. 440; 7-9 paratype No. 441.

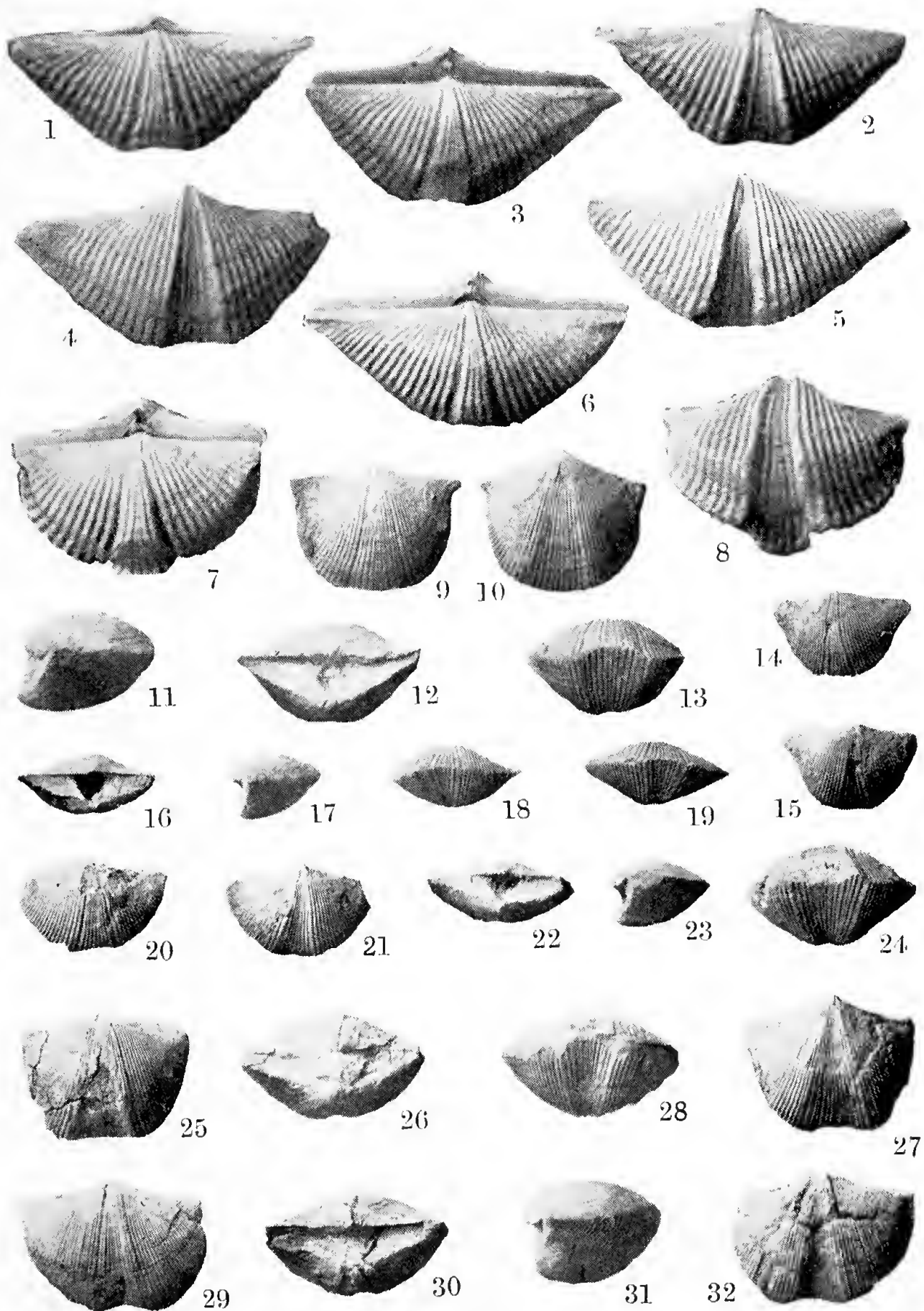


PLATE 3

1-8—*Austrospirifer variabilis* Glenister, n.gen., n.sp. All figures x 2. 1-2, hypotype No. 453; 3-4, hypotype No. 454; 5-6, hypotype No. 455; 7-8, hypotype No. 456.
 9-32—*Cyrtospirifer minilyacensis* Glenister, n.sp. All figures x 1. 9-13, holotype No. 477; 14-18, hypotype No. 457; 19-23, hypotype No. 458; 24-27, hypotype No. 459; 28-32, hypotype No. 460.

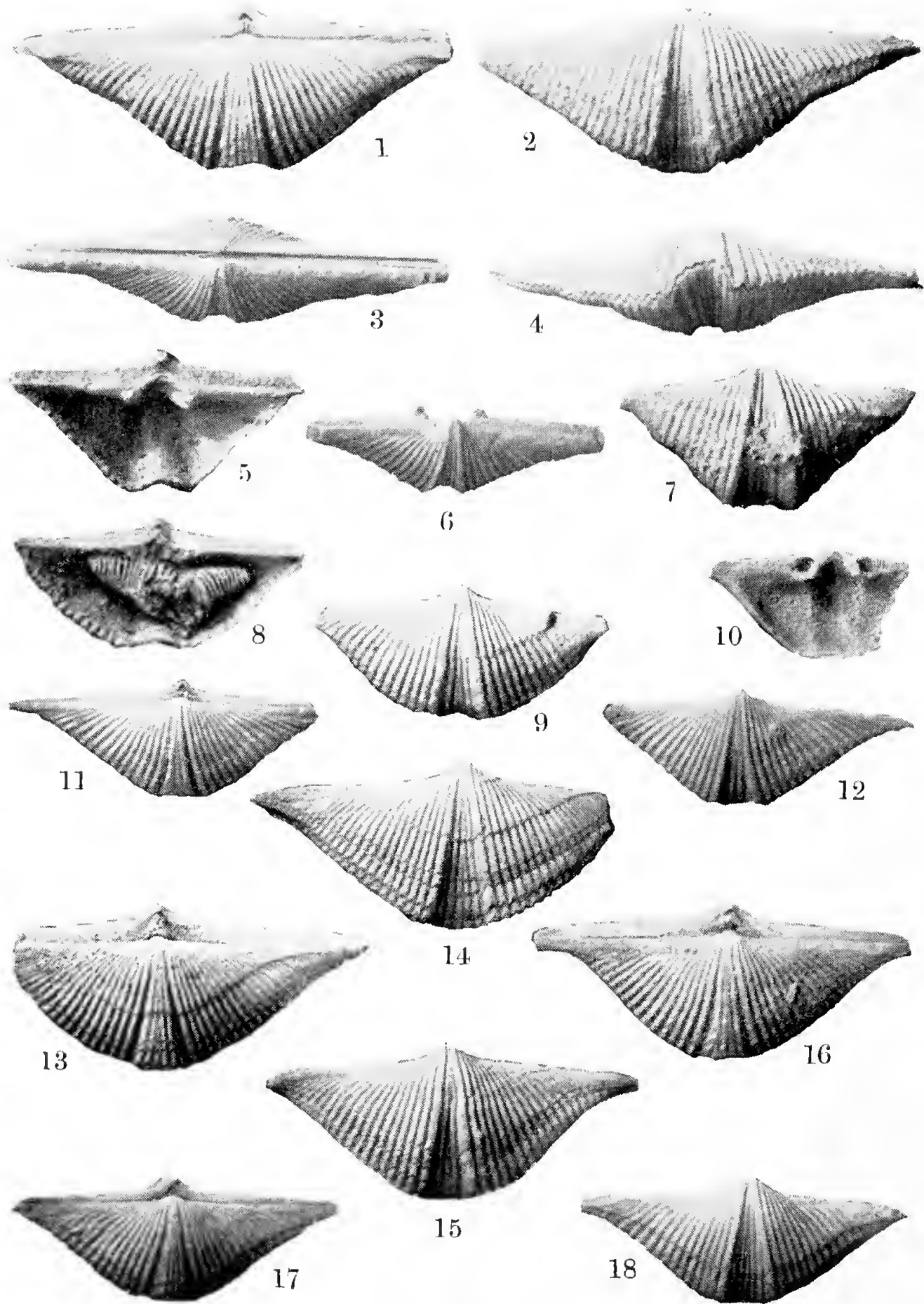


PLATE 2

1-18—*Austrospirifer variabilis* Glenister, n.gen., n.sp. All figures x 2. 1-4, holotype No. 426; 5-7, paratype No. 434; 8, paratype No. 436; 9-10, paratype No. 435; 11-12, hypotype No. 449; 13-14, hypotype No. 450; 15-16, hypotype No. 451; 17-18, hypotype No. 452.

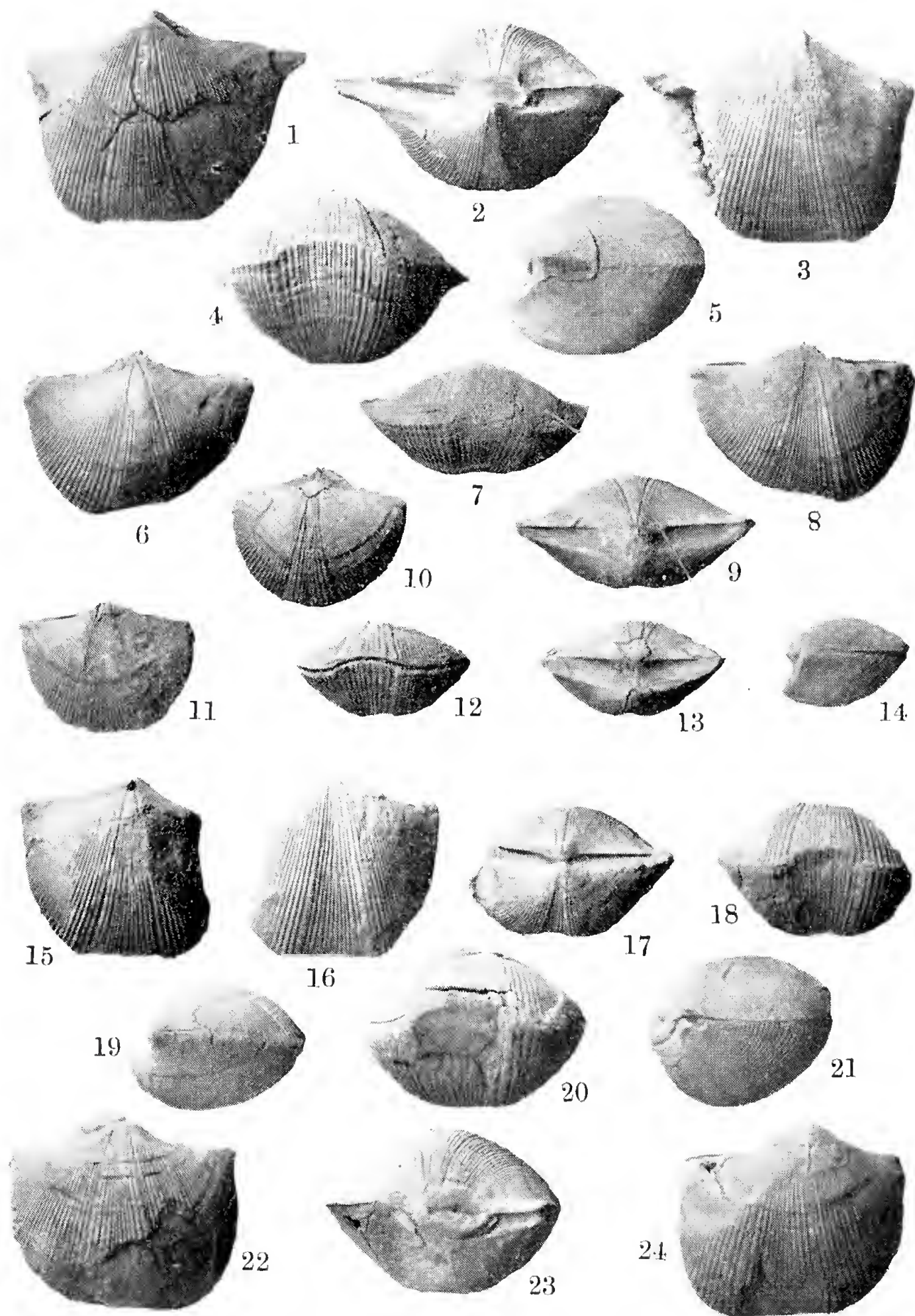


PLATE 4

1-24—*Cyrtospirifer australis* Glenister, n.sp. All figures x 1. 1-5, holotype No. 427; 6-9, hypotype No. 461; 10-14, hypotype No. 462; 15-19, hypotype No. 463; 20-24, hypotype No. 464.

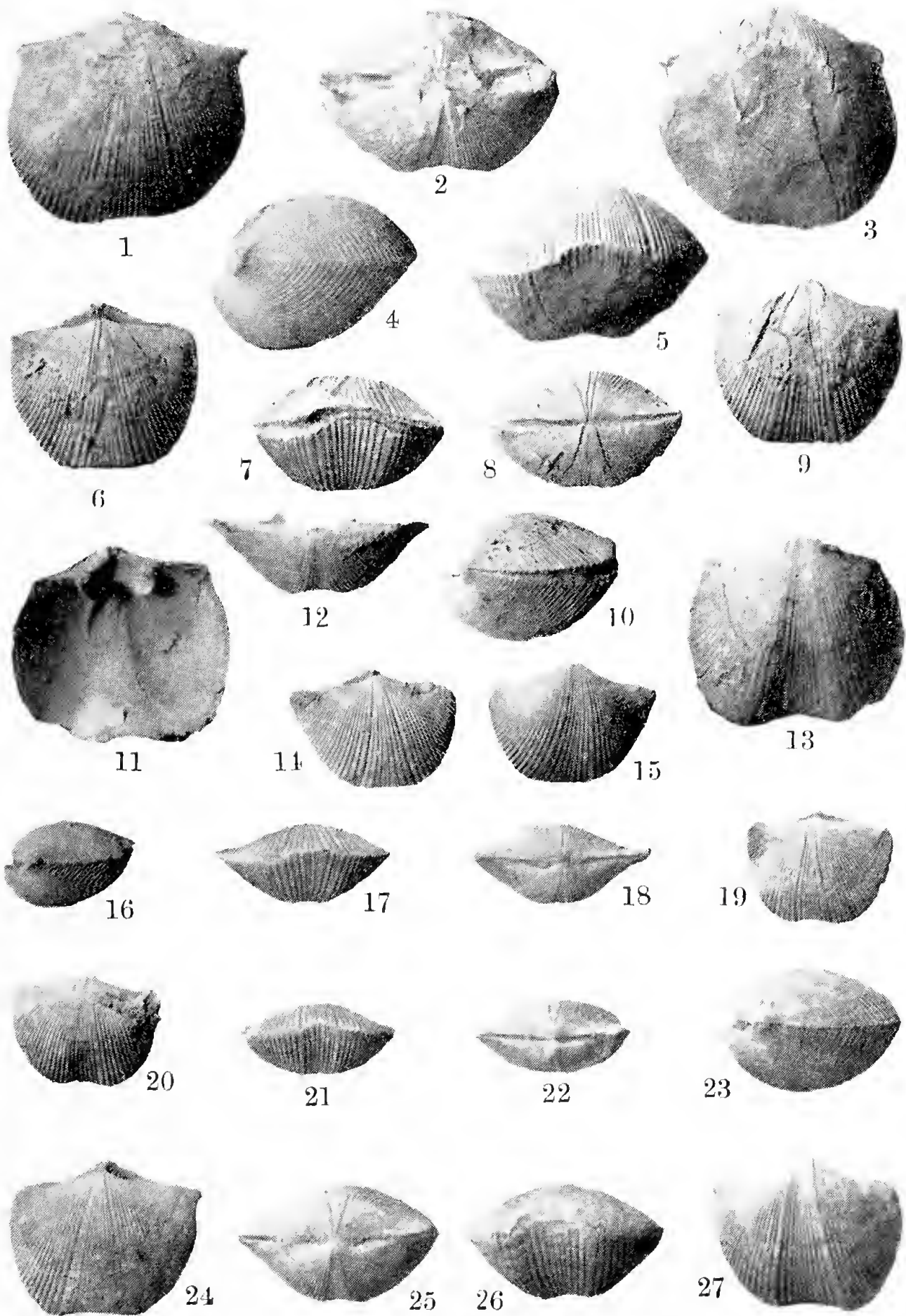


PLATE 5

1-5—*Cyrtospirifer australis* Glenister, n.sp. All figures x 1. Hypotype No. 465.
 6-27—*Cyrtospirifer gneudnaensis* Glenister, n.sp. All figures x 1. 6-10, holotype No. 428;
 11-13, paratype No. 443; 14-18, hypotype No. 466; 19-22, hypotype No. 467; 23-27, hypotype No. 468.

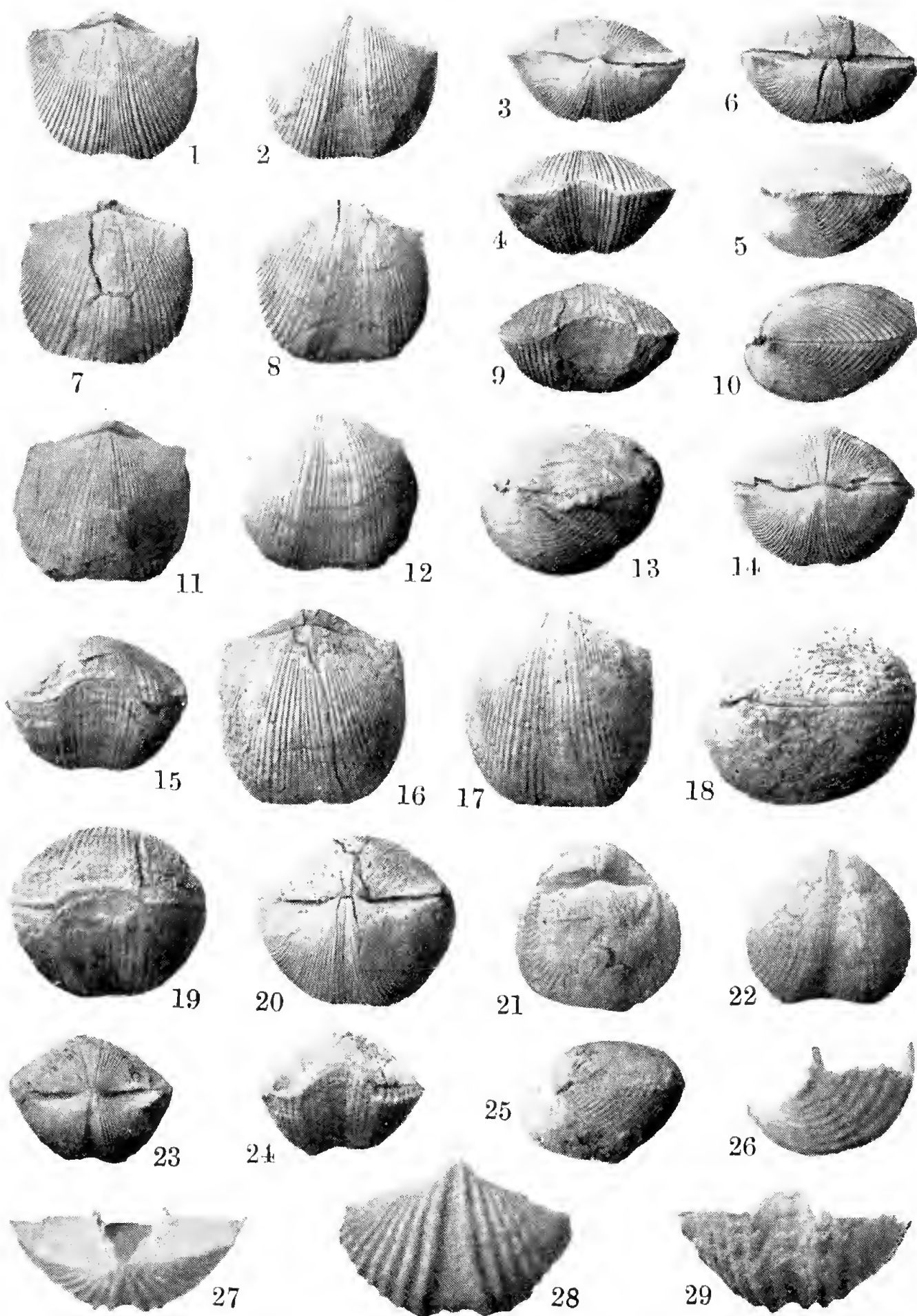


PLATE 6

1-20—*Cyrtospirifer gneudnaensis* Glenister, n.sp. All figures x 1. 1-5, hypotype No. 469; 6-10, hypotype No. 470; 11-15, hypotype No. 471; 16-20, hypotype No. 472.

21-25—*Cyrtospirifer brevicardinis* Glenister, n.sp. All figures x 1. Holotype No. 429.

26-29—*Punctospirifer plicatosulcatus* Glenister, n.sp. All figures x 2. Holotype No. 431.

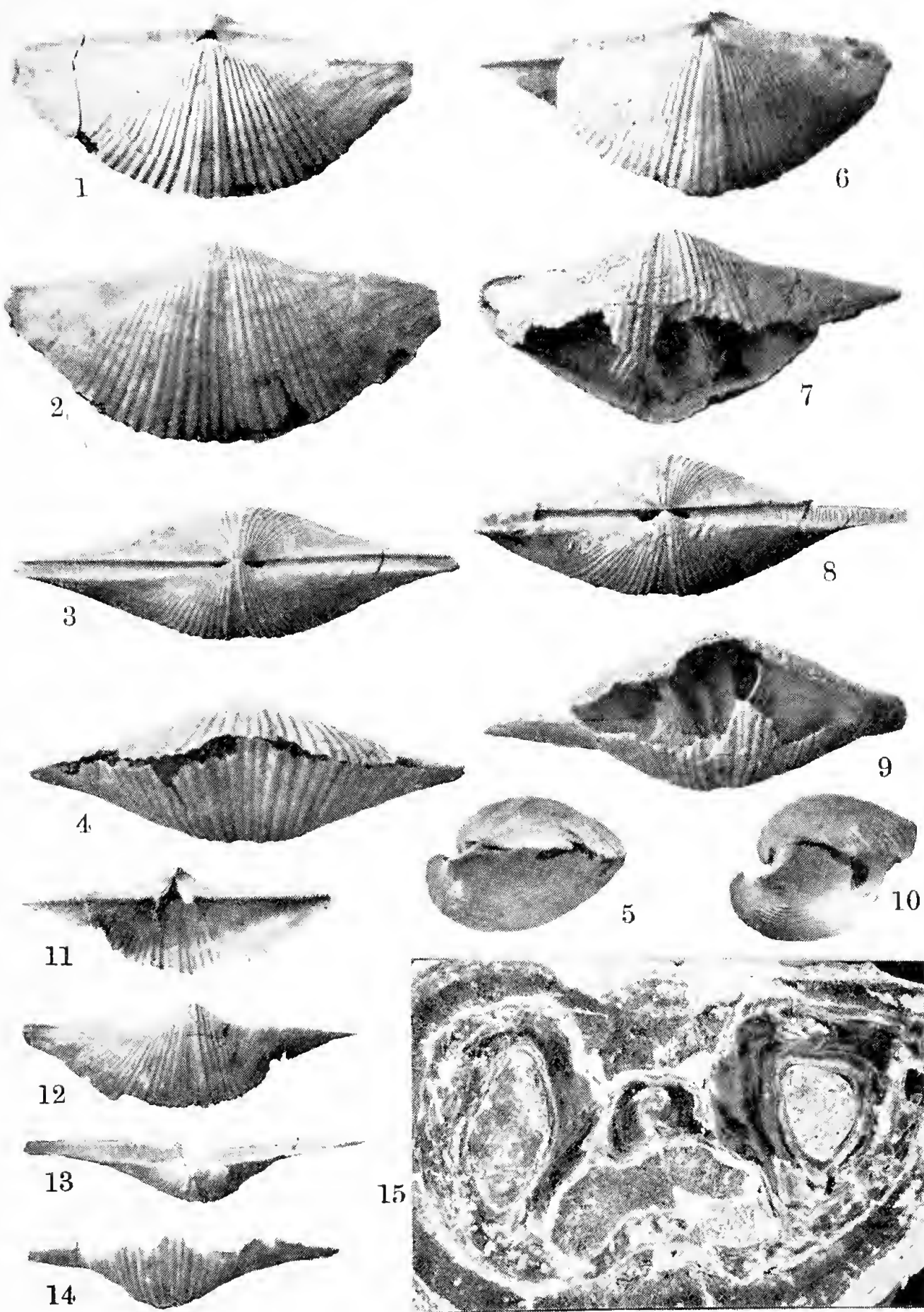


PLATE 7

1-14—*Spirifer fluctuosus* Glenister, n.sp. All figures x 1. 1-5, holotype No. 430; 6-10, paratype No. 479; 11-14, paratype No. 445.

15—*Syringothyris spissus* Glenister, n.sp. Paratype No. 480, x 3. The figure is a photographic positive produced by using a celluloid peel as a photographic negative.

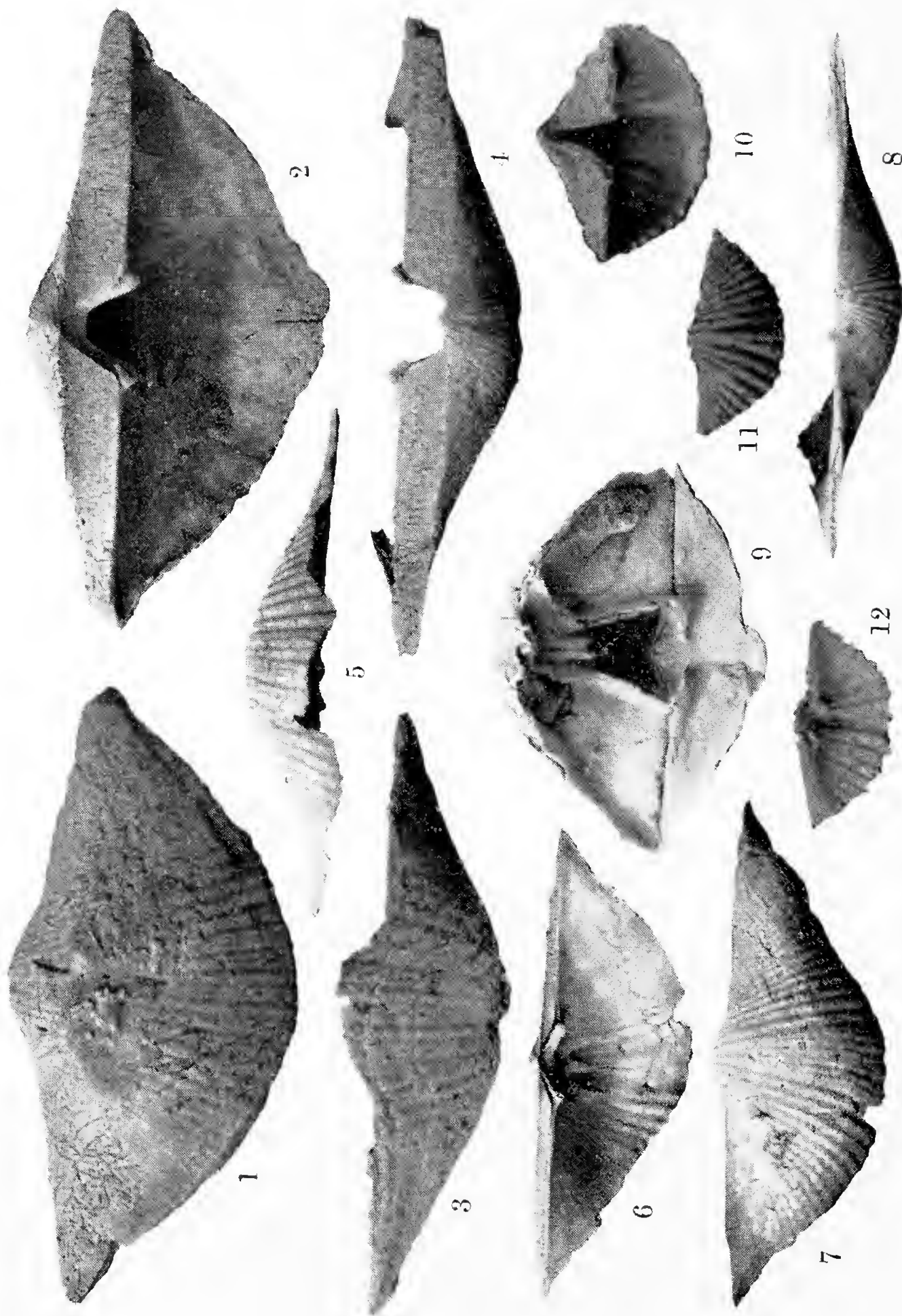


PLATE 8

- 1-8—*Spirifer fluctuosus* Glenister, n.sp. All figures x 1. 1-4, paratype No. 446; 5-8, paratype No. 444.
 9—*Syringothyris spissus* Glenister, n.sp. Holotype No. 432, x 1.
 10-12—*Punctospirifer plicatosulcatus* Glenister, n.sp. All figures x 2. 10, holotype No. 431; 11-12, paratype No. 447.

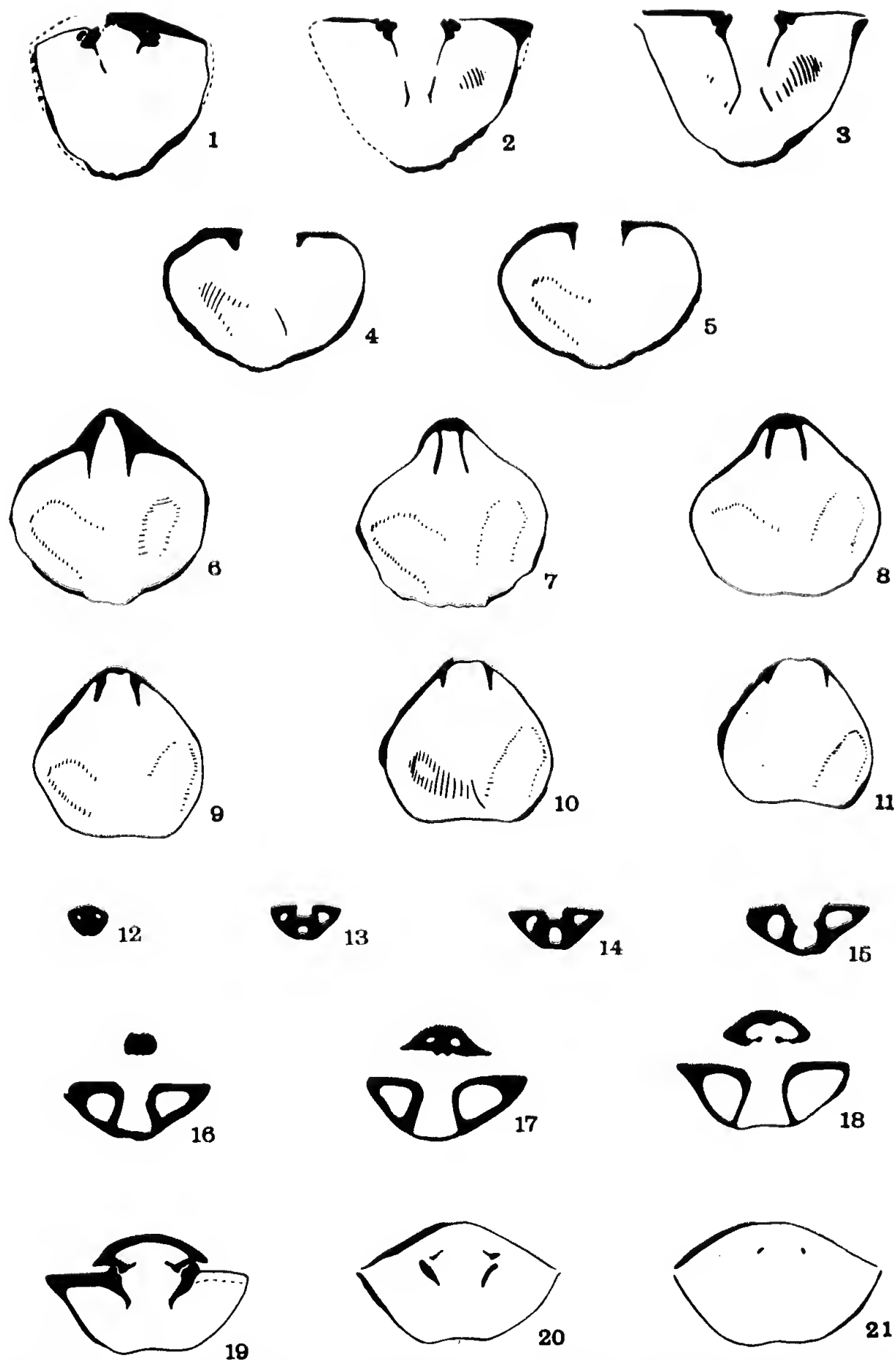


FIG. 5.—1-21—*Cyrtospirifer minilyaensis* Glenister, n.sp. Serial sections drawn onto photographic positives produced by using the celluloid pulls as photographic negatives, x 1.2 (approx.). 1-11, sections of paratype No. 438 taken parallel to the plane of commissure: 1-3 at 0.5 mm. intervals, 4-11 at 1 mm. intervals. 12-21, sections of paratype No. 437 taken at 1 mm. intervals at right angles to the plane of commissure.

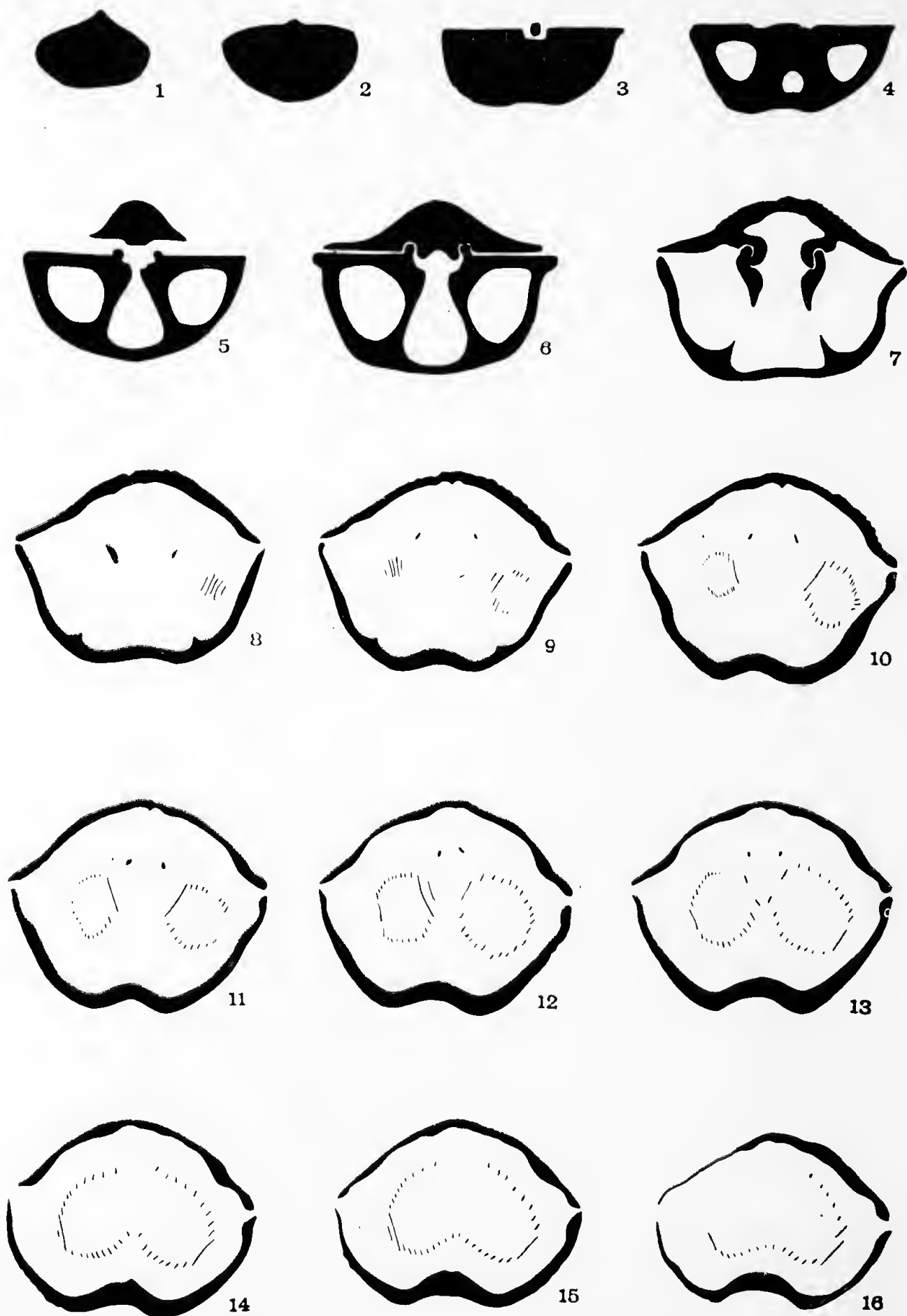


Fig. 6.—1-16—*Cyrtospirifer brevicardinis* Glenister, n.sp. Serial sections taken at 1 mm. intervals from paratype No. 478 at right angles to the plane of commissure, x 2 (approx.). The figures were drawn onto photographic positives, made by using the celluloid serial sections as photographic negatives.

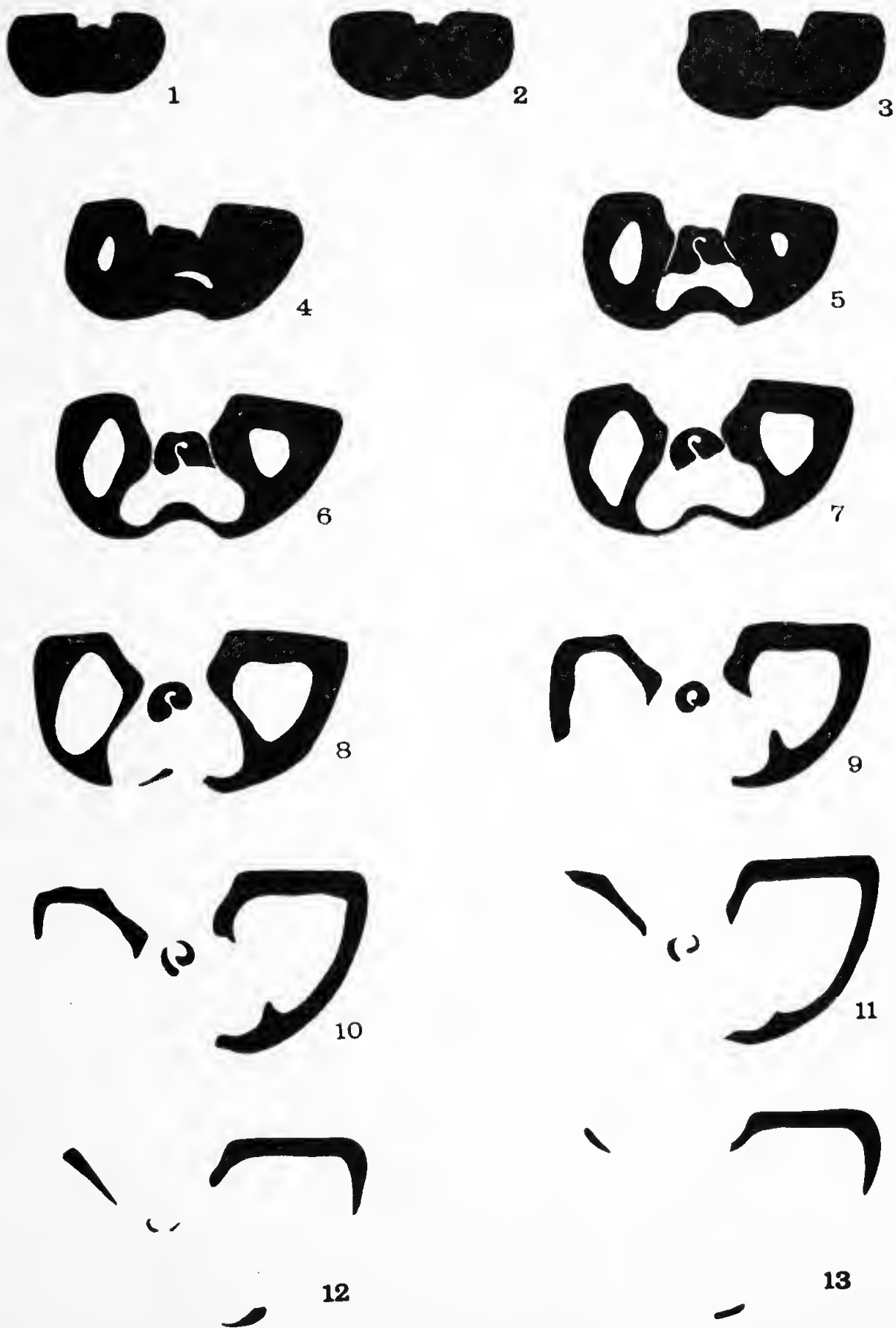


Fig. 7-1-13—*Syringothyris spissus* Glenlster, n.sp., Serial sections taken at 1 mm. intervals from paratype No. 480 at right angles to the plane of commissure, x 1.5 (approx.). The figures were drawn onto photographic positives, made by using the celluloid serial sections as photographic negatives.

Successive planes were etched with 5 per cent. hydrochloric acid, and a celluloid peel taken at each, using the dry peel technique outlined by Sternberg and Belding (1942). A small vice with felt-lined jaws was used to clamp the moistened surface of the celluloid sheet to the etched surface of the fossil. By using considerable pressures in the vice, it was found that less solvent could be used on the celluloid sheet. Peels were thus ready for removal in three to four minutes. The celluloid used was equal in thickness to the section interval. Thus when the celluloid peels are superimposed in their correct order, they give a three dimensional model of the fossil.

Photographic positives were made, using the celluloid peels as negatives (Plate I). Ink drawings of the organic structures were then traced directly on to the photograph, and the photographic images dissolved when the ink dried. The line drawings of the serial sections were then ready for mounting.

Practically the whole fauna of the Carboniferous Moogoorec Limestone has suffered at least surface silicification. Many of the brachiopods have had their shell substance completely replaced by silica in such a manner that the finest structural details are faithfully preserved. Large blocks of limestone were collected and the fossil content freed in an acid bath.

Classification of the Spiriferidae

During the last quarter of a century, four substantially new classifications of the Spiriferidae have been proposed (Frederiks, 1926; Schuchert and Le Vene, 1929; Paeckelmann, 1931; Termier and Termier, 1949). They have little in common, since each is based on different interpretations of the relative taxonomic value which can be applied to the various morphological shell features. Modern authors have as a rule accepted the classifications of either Frederiks, Schuchert and Le Vene, or Paeckelmann, and with the notable exceptions of George (1933) and Termier and Termier (1949), no serious attempt has been made to question either the utility or the phylogenetic coherency of these classifications.

The three classifications mentioned above are alike in their approach to the problem. Each is purely morphological. They differ only in the morphological features chosen as being of taxonomic value, and the consistency with which the taxonomic criteria are applied. Frederiks (1926) presented a classification which is unrivalled in simplicity, consistency of application, and artificiality. He devised a reticulum with the ordinate and abscissa represented by the type of morphic features developed in the rostral area, and the type of shell ornamentation. Known genera were placed in their appropriate pigeon-holes. By choosing such a simple network of co-ordinates, Frederiks was forced to confine his use of taxonomic features to those represented by the two co-ordinates. Groups previously defined on features other than those used by him were readjusted to fit the reticulum, thereby losing much of their original meaning. The morphological criteria which form the basis of the classification presented

by Schuchert and Le Vene (1929) are not expressly stated. An examination of this work reveals that a wide variety of morphic features is utilised. Despite the variety of features used, the classification is entirely morphogenetic and takes only scant account of the phenomenon of homeomorphy, which is so common amongst the Spiriferidae. Paeckelmann's (1931) approach was again partly morphogenetic. Punctuation and jugal structures were considered to be of major taxonomic importance. The artificiality of such treatments becomes evident when the taxonomic units which result from them are compared. Corresponding sub-families are so dissimilar that the names lose practically all meaning, and if the classifications are to be rigidly followed, the scope of many genera must be altered.

Numerous abortive attempts have shown that morphogenetic classifications are of necessity static; with difficulty they may be so constructed that they satisfactorily embrace most known facts, but they can not be made sufficiently complex to accommodate new material. The only taxonomic groups which are sufficiently flexible to include new units are purely phylogenetic. The classification of such a diverse group as the Spiriferidae cannot become stable until it is founded on a phylogenetic basis. Only then can the problem of frequent homeomorphy be overcome. An attempt in this direction has recently been made by Termier and Termier (1949). Their classification is the most satisfactory yet proposed.

Phylogeny can of course, be traced only by reference to the evolving morphological features. The problem of deciding which morphological features present traceable lines of development immediately presents itself. In deciding this question, it must be remembered that different features can not be expected to evolve at the same rate. The degree of stability of any structural feature may also vary within a group when the group is considered over a long period.

The remaining part of this section will be devoted to a consideration of the relative taxonomic value of the more important morphological features of the Spiriferidae. It must however, be remembered, that the relative stability of any morphological feature may vary between different evolving stocks. It is also necessary to again stress that the degree of morphological stability generally varies through wide limits within a particular group when that group is considered over a long period of time. Thus many of the statements made below are of necessity generalisations.

Internal Structures.—Without doubt the most stable feature of the spiriferid shell was the form of the brachidium. From the Silurian to the Triassic the spiralia remained sufficiently constant in form to defy any attempt to split the family on this feature. In some genera the spiralia of the brachidium remained separated, but in more advanced genera they were joined by the ultimate fusion of the jugal processes. The stage of development of the jugal processes is often difficult to determine, but this feature seems to be of considerable taxonomic value.

Dental lamellae developed independently in many spiriferid groups, but they nevertheless form a valuable criterion for tracing evolutionary lines. Many genera may be clearly defined by reference to some modification of the dental lamellae. Thus *Cystina* possesses strong dental lamellae which fuse ventrally to form a spondylium, *Cyrtospirifer* has its well-developed subdelthyrial platform, and *Spirifer* s.s. is characterised by short thick dental lamellae which are confined to the rostral area of the shell. An interesting modification of the dental lamellae is seen in *Syringothyris*. Here the inner layer forms a subdelthyrial platform as in *Cyrtospirifer*. However, in the plane of symmetry where the two components of the subdelthyrial platform meet, the distal edge of each component is rolled to form an anteriorly projecting closed tube, the syrinx. (Plate 15—8; plate 8—9; fig. 6.). The inner surface of the syrinx is composed of radially arranged lamellae, suggesting that this structure served as an area of muscle attachment. Median septa are frequently developed in both valves, but they are of limited taxonomic value, since they tend to be obliterated in the late ephebic growth stage by the development of rostral callosities. The nature of the socket plates is often difficult to detect, but is doubtless of taxonomic value. The diverse types of socket plates are illustrated by *Cyrtospirifer*, *Spirifer* s.s. and *Austrospirifer*. The socket plates of *Cyrtospirifer* are not directly supported by lamellae beneath them, while those of *Austrospirifer* and *Spirifer* are supported to the extent that the sockets appear as pits in the posterior shell wall. *Spirifer* has long narrow sockets, while the sockets of *Austrospirifer* are uniformly hemispherical. The development of an apical callosity is of limited value in defining some genera, but is useless in tracing phylogeny. Many genera never develop thickened shells, and those which do, rarely exhibit rapid shell secretion in the rostral area until the late ephebic and gerontic growth stages.

General Form.—The general shell shape of the spiriferids is a feature which is particularly susceptible to homeomorphy. A study of the growth lines also shows that the shell index (the ratio of width along the hinge line to the length of the valve, measured in the plane of symmetry along the shell surface) varies within wide limits during ontogeny. From these facts it becomes obvious that the shell outline attained by an individual at the time of death is of little taxonomic value. However, a study of closely related species often reveals that the ontogenies of the shell outlines are similar, and that the outlines attained at maturity are dissimilar due only to a relative retardation in development of certain species. In the four species of *Cyrtospirifer* described below, the growth lines around the umbo show that the shells were brachythyrid in the nepionic growth stage. Neanic shells were megathyrid, with alate cardinal extremities. The ephebic and gerontic growth stages are marked by vigorous growth around the anterior and anterio-lateral margins and a virtual cessation of growth along the hinge line. Mature specimens thus lose their alate neanic outline and become either subquadrate or even brachythyrid. This comparison

of shell outlines throughout ontogeny has proved to be of greater value than merely comparing them at some arbitrarily chosen growth stage such as at the time of death.

High cardinal areas have developed in many different spiriferid groups. Moreover, the height of the cardinal area may vary between species which are otherwise closely related. Grabau's closely knit group of "*Sinospirifer*" *sinensis* contains forms which show an almost continuous range from the high cardinal area of *Tenticospirifer tenticulum* to the extremely narrow cardinal area of *Sinospirifer sinensis* (mut. *alpha*). It would seem then that the degree to which the cardinal area is developed is of limited taxonomic value.

Ornamentation.—The types of ornamentation developed by the spiriferid stock are extremely diverse. Most genera can be clearly differentiated by their macro-ornamentation, and although evolutionary trends are not fully understood and homeomorphy is certainly common, this criterion seems to be of taxonomic value. The plications of the fold and sinus have been singled out for special attention by several authors, including Grabau (1931) and Gatinaud (1949, a-d). In consideration of the detailed methods used by Grabau and Gatinaud, the present author has come to the conclusion that although the ornamentation of the sinus is of considerable taxonomic value, it does not warrant the detailed treatment given by these two authors. Grabau's method was qualitative. He differentiated new species and genera using fine details of plication arrangement as the most important, and indeed in some cases the only taxonomic criterion. The artificiality of these divisions is evident when it is noted that the arrangement of plications may differ widely from one side of the sinus to the other. Depending largely on previously published figures and plates, Gatinaud carried the splitting of the plicate spiriferids to a new extreme level. His work was quantitative, some of his new formulae containing as many as 35 individual factors. Some of the factors are entirely dependent on the growth stage reached by the specimens. Since the growth stage can not be accurately determined, the formulae merely succeed in splitting material into numerous artificial units in which the variability due to the ontogenetic stage reached and true interspecific variation are confused.

Orton (1914) and Termier and Termier (1949) have suggested that the presence or absence of a fold and sinus bears a relation to the intensity of respiratory exchanges, and is thus of considerable taxonomic value. Fossil groups at least do not contradict this belief, although evolutionary trends in the development of the sinus are difficult to determine. The point of origin of the sinus is of value in separating genera. Thus *Cyrtospirifer* and *Theodossia* are almost identical except that in the former the sinus originates at the beak, whereas it originates at about the mid-length of *Theodossia*. The presence of papilose, granulose and spinose ornamentation is valuable in generic definitions, although subject to frequent homeomorphy.

Punctuation.—The attention of brachiopod workers has recently been focussed on the fine details of shell structure, since Cooper (1944) proposed a classification of the Articulata based largely on the presence or absence of punctuation. The division of the Articulata into Palaeotremata, Protremata and Telotremata was replaced by a grouping into Palaeotremata, impunctate Articulata, pseudopunctate Articulata, and punctate Articulata. Cooper's classification results in the splitting of the Spiriferidae of King. The impunctate spiriferids are included in the Spiriferacea (emend Cooper) and the punctate spiriferids in a new superfamily, the Punctospiracea. If this classification has any phylogenetic basis, it implies the development of a truly remarkable series of homeomorphs. The present author finds it difficult to believe that an exceedingly complex structure such as the spiriferid brachidium could develop independently in two distantly related phylogenetic lineages; namely from both punctate and impunctate stocks. It seems more reasonable to assume that the presence or absence of punctuation is only of secondary phylogenetic importance. The latter assumption is strengthened by the occurrence of both punctate and impunctate forms within two other groups which in all other morphological features appear to constitute natural phylogenetic divisions. These are the Orthida, which contain the punctate Dalmanellacea, and the Rhynchonellida, which include the punctate Rhynchoporacea. The existence of the punctate Terebratulida is also significant. To assume that the punctate brachiopod groups developed from a single common stock and that the closely similar impunctate groups are a series of homeomorphs which developed from an independent stock is unreasonable.

The Western Australian material provides evidence which has an important bearing in the discussion of phylogenetic significance of punctuation. A new species described below as *Syringothyris spissus* is a typical species of *Syringothyris*, except for the impunctate nature of the shell substance. The syrinx is well developed, and appears to be identical in structure with the same morphological feature of other species of *Syringothyris*. The present author is unable to believe that forms bearing such complex structures as a syrinx and laterally directed spiralia could develop simultaneously in two distantly related phylogenetic lineages. It must then be concluded that the presence or absence of punctuation can not be regarded as of major taxonomic significance.

Closure of the Delthyrium.—In Beecher's classification, the method of closure of the delthyrium was the main feature by which the Articulata were divided into the Protremata and Telotremata. The delthyrium of the Protremata was supposedly restricted by the secretion of a single plate, the pseudodeltidium, which was at first situated posterior to the pedicle. Beecher considered that in the Telotremata the delthyrium was partially closed by the secretion of a pair of deltidial plates, one on either side of the delthyrium. The discovery of deltidial plates among the Protremata (Termier and Termier, 1949) and the presence of a

pseudodeltidium in many spiriferids, has made obvious the artificiality of this division into Protremata and Telotremata.

The delthyrial closing apparatus of the Spiriferidae is quite unsatisfactory in the determination of phylogenies. In a great many specimens the plate or plates are unknown. They were probably dislodged soon after death, and dispersed before the enclosure of the shell in the sediment. Most species in which the plates are definitely known exhibited a protrematous type of delthyrial closure, but some species are known to develop deltidial plates. Termier and Termier (1949) have reported deltidial plates in *Spinocyrtia*, and many specimens of *Neospirifer* in the author's collections clearly show typical deltidial plates. It is thus apparent that at our present state of knowledge of the plates which restrict the delthyrium, these structures are of little value in the taxonomy of the Spiriferidae.

To sum up, the Spiriferidae is considered to be a monophyletic group characterised by the form of the brachidium. It has been subjected to frequent homeomorphy, so that no single morphological feature can be used to completely trace the lines of descent. It is suggested that lines of descent can only be traced with reference to all available morphological and stratigraphical data. Only then can the homeomorphs be separated, and small groups of closely related genera linked in natural lineages.

Systematic Descriptions

Devonian

Family Spiriferidae King, 1846

Subfamily Spiriferinae Schuchert, 1913

Genus *Austrospirifer* Glenister, n. gen.

Type Species.—*Austrospirifer variabilis* Glenister, n. sp.

Description.—This genus is proposed for small, sub-equally biconvex, completely costate, impunctate spiriferoids with uniplicate anterior commissure. The hinge is always the widest part of the shell. The width is generally much greater than the length, but the shell ratio may approach unity in very young or gerontic specimens.

The palintrope of the pedicle valve is narrow, orthocline to gently apsacline, and narrows only slightly towards the cardinal extremities. The broadly triangular delthyrium is almost completely closed by an imperforate convex pseudodeltidium. Dental lamellae are thick and attached to the posterior wall of the shell with little or no development along the floor of the valve. A median septum traverses the posterior part of the muscle scar on the pedicle valve.

The brachial valve bears a narrow, anacline palintrope. Socket plates are thick and supported along their whole length. They enclose hemispherical sockets. The descending lamellae are straight and converge slowly to the points where they are attached to the posterior-

laterally directed, uniformly conical spiralia. Jugal processes are not developed. A low median septum traverses the posterior half of the floor of the brachial valve.

Affinities.—*Austrospirifer* is closely related to a number of Upper Devonian spiriferids, some of which have ranges extending into the Middle Devonian. *Cyrtospirifer* is distinct because of its strong dental lamellae extending along the floor of the valve, and the absence of supporting lamellae under the sockets. *Mucrospirifer* has either an unmodified fold and sinus, or a single costa in the sulcus, while *Acrospirifer* has a non-plicate fold and sinus. *Spirifer sensu stricto* is distinct in having long but narrow sockets, and in the development of jugal processes.

Austrospirifer variabilis Glenister, n. sp.

Plate 2—1-18; Plate 3—1-8; Fig. 1—1-4; Tables II and III.

Description.—The holotype, 4 paratypes and 200 specimens belonging to this species, were available to the author. The two valves are subequally biconvex. Growth lines show that the shell was subquadrate and only slightly wider than long in the immediately post-embryonic stage. The early neanic stage of growth was marked by extreme development along the hinge line, so that the width often measured more than three times the length of the conch. The cardinal extremities were so delicate that they are seldom preserved complete. The ephebic stage is indicated by a retardation of development along the hinge line, and a marked increase in the length and convexity of the valves. Practically no increase in the width of the hinge line takes place in the gerontic stage, but growth continues along the anterior and anterior-lateral margins, so that some specimens have shell indices closely approaching unity. The anterior commissure is strongly uniplicate.

TABLE II

Measurements (in mm.) of *Austrospirifer variabilis* Glenister, n.gen., n.sp.

Growth stage	Neanic		Ephebic				Gerontic		
Catalogue Number †	449	450	426 *	451	452	453	454	455	456
Plates	2—11-12	2—13-14	2—1-4	2—15-16	2—17-18				
Figures	1—1	1—2	1—3			1—4			
Height of pedicle valve	9.0	13.1	13.0	12.3	9.8	10.7	12.4	11.9	12.5
Length on curvature (centre)	10.8	15.5	17.6	14.8	13.1	14.6	17.3	16.5	19.5
Height of brachial valve	8.0	10.6	10.5	9.9	8.4	9.5	9.9	9.7	10.2
Length on curvature (centre)	9.1	12.1	12.3	11.0	9.8	11.2	11.3	11.7	13.8
Width along hinge line	26.4	33.8	36.2	30.4	26.6	25.4	28.4	26.6	20.0
Maximum height of palintrope	2.4	2.7	2.4	2.2	1.6	1.6	2.4	2.1	2.5
Thickness of shell	5.4	6.5	8.3	6.5	6.5	7.6	8.4	8.0	9.5
Maximum width of sinus (anterior)	3.7	5.2	5.6	4.8	4.5	5.9	5.3	4.9	6.1
Number of lateral plications	13	23	20	16	14	11	15	17	13
Shell index of pedicle valve	2.44	2.18	2.06	2.05	2.03	1.74	1.64	1.61	1.02
Shell index of brachial valve	2.90	2.79	2.94	2.76	2.71	2.27	2.51	2.27	1.45

* Holotype.

† These, and succeeding catalogue numbers, refer to the type catalogue of the Bureau of Mineral Resources.

TABLE III

Shell indices for the pedicle valve of *Austrospirifer variabilis* Glenister, n.gen., n.sp.
Measurements measured on growth lines in mm.

Catalogue number	450							454				
Growth stage	Nep.		Nea.					Nep.	Nea.		Eph.	Ger.
Length on curvature (centre)	2.3	3.3	8.2	11.6	12.7	14.8	15.5	4.3	9.0	11.5	13.3	17.5
Corresponding width along hinge line	4.1	6.4	26.2	32.8	33.4	33.6	33.8	7.0	21.8	28.0	28.2	28.4
Shell index	1.78	1.94	3.20	2.83	2.47	2.27	2.18	1.63	3.11	2.43	2.12	1.64

A well-defined deep sinus extends along the pedicle valve from the beak to the anterior margin. The sides of the sinus are steep and the floor is narrowly rounded. At the anterior margin the sinus is produced into an angular

extension which truncates the fold of the brachial valve. The umbo is not prominent and is only slightly recurved. The palintrope is narrow, tapering in width only slightly towards the cardinal extremities. It is flat or weakly

concave and ranges in aspect from orthocline to gently apsacline. Growth lines running parallel to the hinge line are occasionally preserved. A flatly triangular delthyrium bisects the palintrope. It is partially closed by a convex imperforate pseudodeltidium. The pseudodeltidium never completely closes the delthyrium, since a triangular fissure is invariably present in the base of the delthyrium.

The umbo of the brachial valve is weakly developed. At the posterior margin of the brachial valve the fold is not prominent, but towards the anterior margin, especially in mature specimens, it is strongly elevated, having almost vertical sides and a gently convex crest. The palintrope is narrow and anacline in all growth stages.

Internally the pedicle valve bears two thick dental lamellae which support the teeth. They are attached to the posterior margin of the valve, and extend along the floor for a short distance as low ridges. The dental lamellae converge to form a poorly developed subdelthyrial platform just below their mid-height. A shallow rostral cavity appears on the lateral side of each dental lamella, as well as beneath the delthyrial platform. Accelerated secretion of shell material in the gerontic growth stage tends to obscure these features. The muscle scars lie in a deep pit situated in the posterior half of the valve. The posterior part of this pit is traversed by a median septum.

The socket plates are thick, and attached to the floor of the brachial valve for their whole length. They enclose a pair of large hemispherical sockets. The descending lamellae are straight and converge slowly to the points where they are attached to uniformly conical, posteriorly directed spires without being supported by a jugum. The area of muscle attachment is confined to a pit in the posterior half of the shell. It is bounded by a pair of arcuate grooves and traversed by a low median septum. The cardinal process is composed of numerous thin lamellae arranged approximately parallel to the plane of symmetry.

From 10 to 23 radially arranged plications have been observed on either side of the sinus. Bifurcation of these lateral plications is unknown. The fold and sinus bear from 2 to 6 plications. The occurrence of plications between the bounding plications and the primary plications is rare. In no case has bifurcation of the sinal plications been observed. Both plications and interspaces are covered with fine longitudinal striations. These become particularly prominent along the mid-line of the sinus, probably due to the better preservation of this area. The interspaces are broader than the plications. Sinal plications are finer than the lateral plications.

The species name refers to the strikingly wide variation of shell form encountered in this species.

Occurrence.—All types are from locality 200* in the Gneudna Limestone, 3.5 miles south of Gneudna Well, Williambury Station, North-West Basin, Western Australia.

Repository.—Holotype No. 426, paratypes Nos. 423-436, and hypotypes Nos. 449-456 are lodged with the Bureau of Mineral Resources, Geology and Geophysics, Canberra.

Subfamily **Cyrtospiriferinae** Termier and
Termier, 1949

Genus **Cyrtospirifer** Nalivkin, 1918

In 1918 Nalivkin established *Cyrtospirifer* as a new subgenus of *Spirifer*, with *Spirifer verneuili* Murchison as type species. Many recent authors have accorded full generic rank to the group of *Spirifer verneuili*. There can be no doubt that this practice is justified, since fundamental morphological differences occur between the group of *Spirifer striatus*, the type species of *Spirifer*, and the group of *Spirifer verneuili*. The dental lamellae of *Cyrtospirifer* are primitive in that they extend anteriorly along the floor of the pedicle valve for a considerable distance. The two dental lamellae are also joined at about their mid-height by a well developed subdelthyrial platform. The dental lamellae of *Spirifer* s.s. are confined to the rostral area, and a delthyrial platform is never well developed. Substantial differences in the form of the descending lamellae and development of the jugal process also appear to exist between the two genera, but insufficient information is at present available for them to be stated with any degree of certainty. Obvious differences occur in the macro-ornamentation. *Cyrtospirifer* has numerous fine plications. They are simple on the flanks, but complexly bifurcated and intercalated in the fold and sinus. *Spirifer* s.s. has fewer plications on both the flanks and the sinus. They are usually simple on the flanks, but in the lower Pennsylvanian strong fasciculate costae begin to develop. This evolutionary trend culminates in the Pennsylvanian and Permian genus *Neospirifer*, a form with weakly developed dental lamellae and strongly fasciculate ribs on the flanks. *Spirifer* and *Cyrtospirifer* are also separated stratigraphically. *Cyrtospirifer* is known only from the Frasnian, while *Spirifer* s.s. is probably confined to the Mississippian and lower Pennsylvanian, although there are doubtful reports of its occurrence in the Upper Devonian. *Neospirifer* first appears at the base of the Pennsylvanian and continues throughout the Permian.

Since Nalivkin established *Cyrtospirifer*, there have been many attempts to set up other subgenera of *Spirifer*. The object of this practice has in many cases been to emphasise the presence of large morphological series which are not sufficiently different from other geographically isolated faunules to warrant generic status. Considering the extreme variability characteristic of the Upper Palaeozoic Spiriferidae, it becomes evident that these groups are of dubious value. The creation of subgenera is not common practice amongst students of Palaeozoic brachiopods. Subsequent authors have thus tended to give full generic status to these groups, without critically examining the morphological criteria on which they are differentiated. The new genera and subgenera of spiriferids proposed

*This and succeeding locality numbers refer to the field numbers of the Bureau of Mineral Resources.

by Grabau (1931) and Tien (1938) will be considered, since many of them obviously belong with the group of *Spirifer verneuili* in the genus *Cyrtospirifer*.

In 1931 Grabau proposed *Sinospirifer* as a subgenus of *Spirifer* for the group of *Spirifer sinensis*. He believed these brachiopods to constitute a morphological series whose development and differentiation occurred in the epeiric waters which covered southern China in Upper Devonian times. The Chinese forms were described as possessing "certain characteristics which stamp them as a morphological group (or *Formenreihe*) and enable one readily to distinguish them from most of the related European and American forms." However, the only character which Grabau mentions as being distinctive of the Chinese forms is their small size, although he goes into some detail to explain that the macroscopic ornamentation of the Chinese group is identical with that of the European forms. This fact assumes greater significance in the light of Grabau's statement that the mode and appearance of the sinal plications in the pedicle valve has "definite morphological value and may easily assume the first rank among the variable morphic structures." Many European forms referred to *Cyrtospirifer verneuili* are however, no larger than the average Chinese form, while the Russian forms do not in general appear to be any larger than those found in China. Thus although the *Cyrtospirifer sinensis* group may represent a morphological series, it is almost identical with the groups of *Cyrtospirifer* common in the Upper Devonian of America, Europe, North Africa and Australia. *Sinospirifer* Grabau should then be considered as a subjective synonym of the genus *Cyrtospirifer* Nalivkin, since the accordance of subgeneric status to geographical groups can only produce confused taxonomy.

In 1934 Grabau restricted the subgenus *Sinospirifer* to those forms with two primary sinal plications. The group previously included in *Sinospirifer* but possessing a single symmetrically placed primary sinal plication was separated out as a new sub-genus of *Spirifer*, namely *Centrosprifer*, with *Spirifer chaoi* Grabau as genotype. Substantial variations in the nature of the sinal plications (figs. 1 and 3) are noticeable on many specimens, between one side of the sinus and the other. Intra-specific variation is considerable, and inter-specific variation is pronounced. *Centrosprifer* Grabau is thus to be considered as a subjective synonym of *Cyrtospirifer*, since it was founded on morphological features of no more than specific value.

Tien (1938) further subdivided *Sinospirifer* (emend Grabau 1934), separating out two new subgenera of *Spirifer*, *Tenticospirifer*, with *Spirifer tenticulum* Verneuil as type species, included forms similar to *Sinospirifer* in most respects, but having a hemipyramidal pedicle valve. Other supposedly characteristic features were the thin shell, thin socket plates, absence of calcareous filling matter in the rostral area, and absence of a median septum on the floor of the brachial valve. All gradations of shell

convexity from equi-biconvex to almost plano-pyramidal may be traced in the Chinese group of *Spirifer sinensis*. From the point of view of shell shape the group of *Spirifer tenticulum* then appears to represent extreme forms in a more or less continuous (normal) variation. The other features mentioned as distinctive are largely a function of age, and are certainly of no greater than specific value. The cellulose pull technique used in the present investigation showed the growth lamellae clearly. Cross-sections through the rostral area of the Western Australian specimens showed the contour of the internal surface of the valves to change during ontogeny. Fine morphological features such as the rostral cavity and the dorsal and ventral septa were generally obliterated in the gerontic growth stage by deposition of a thick layer of calcite in the vicinity of the rostral area. *Tenticospirifer* Tien is thus to be considered as a subjective synonym of *Cyrtospirifer*. *Hunanospirifer* (Tien 1938) was proposed as a new subgenus of *Spirifer* with *Spirifer wangi* as type species. *Hunanospirifer* was stated to differ from *Sinospirifer* and *Tenticospirifer* "principally in the feature of the hinge plate which is at first a solid one, being sharply arched above and perfectly flat below, but a little further down, the lower surface of the plate becomes divided in the centre by a small semicircle." The only interpretation which can be applied to this is that the hinge plate thins between the sockets. This occurs almost universally amongst the spiriferids and can not constitute a valid basis for the creation of a new subgenus. *Hunanospirifer* Tien is thus to be considered as a subjective synonym of *Cyrtospirifer*.

Schizospirifer was proposed by Grabau in 1931 as a new subgenus of *Spirifer*, with *Spirifer latistriatus* Frech as type species. Grabau (1931, p. 354) states that Frech's description of *Spirifer latistriatus* is "worthless" but goes on to found *Schizospirifer* on Frech's work together with observations on one poorly preserved specimen in his own collections. Insufficient is known of this Middle Devonian species to correlate it with any existing genus. The presence of coarse bifurcating lateral plications seems to prohibit *Spirifer latistriatus* from being considered as a primitive *Cyrtospirifer*. Further investigation is needed before the subgeneric group of *Spirifer latistriatus* becomes recognisable and can be assigned to some generic group.

Platyspirifer was proposed by Grabau in 1931 for spiriferids similar to the group of *Cyrtospirifer sinensis* but having a hinge line slightly shorter than the maximum width of the shell. He selected *Schizophoria paronai* Martelli as the genotype. The species at present assigned to *Cyrtospirifer* are characterized by extreme variation of both the ratio of length to breadth and the position of greatest width of the shell. Shell ratios also vary markedly during the ontogeny of the individual. With these facts in mind, it is doubtful whether the specimens Grabau groups to constitute *Platyspirifer* even belong to valid species. There can be no doubt that *Platyspirifer* Grabau should be suppressed as a subjective synonym of *Cyrtospirifer*.

Spirifer padaukpinensis Recl. from the Padaukpin Limestone of the Northern Shan States of Burma, was used by Grabau (1931) as the type species of *Indospirifer*, a new subgenus of *Spirifer*. This rather distinct group is known only from the Middle Devonian of Asia. It is not closely related to *Cyrtospirifer*. The ribs of *Indospirifer* are far less numerous than those of *Cyrtospirifer*. They bear numerous fine striae which begin in the grooves and diverge fanwise onto the ribs, where they disappear. The internal structures are unknown, but it is probable that future study will prove this group worthy of generic status.

A further middle Devonian group was segregated by Grabau (1931) under the new genus *Plectospirifer*, with *Spirifer (Plectospirifer) peimi* Grabau as type species. The flanks bear coarse ribs, either simple or exhibiting bifurcation. The sinus may be smooth or characterized by finer sinuulations. In the latter case there is usually a single median primary plication. The shell surface is characterized by regular growth lamellae bearing radial striations; this prompted Grabau to place *Plectospirifer* amongst the Reticulariinae of Waagen. Unlike many of the Spiriferidae, *Plectospirifer* has its delthyrium closed in the manner usual amongst Beecher's old group, the Telotremita. The delthyrium is partially closed by a deltidium originating as a pair of discrete plates on either flank of the delthyrium. In many cases shell material is resorbed, so that the pedicle foramen occupies the position of the beak on the pedicle valve. Strong dental lamellae are present, but detailed internal structures are not well known. This group probably represents a valid genus.

Cyrtiopsis was proposed as a new genus by Grabau (1933) with *Cyrtiopsis davidsoni* Grabau as type species. He drew attention to the similarity between *Cyrtiopsis* and the "Upper Devonian Spirifers" and came to the conclusion that *Cyrtiopsis* differed from them "only in the persistence of the pseudodeltidium which moreover is pierced".

In most species of *Cyrtospirifer*, the plates which close the delthyrial openings are unknown. Two narrow grooves, however, invariably appear on the edge of the palintrope, and it seems reasonable to assume that their function was to lodge the plate or plates which closed the delthyrium. Many species of *Cyrtospirifer* have a large delthyrial opening, and it is unlikely that these forms would have survived without some efficient method of sealing that part of the delthyrial cavity not occupied by the pedicle. Closely related forms to those in which this apparatus for closing the delthyrium is not preserved, do in fact, possess a pseudodeltidium (*Cyrtospirifer verneuili* and *Cyrtospirifer brevicardinis*). It thus seems probable that the absence in the fossil state of apparatus for closing the delthyrium does not constitute proof that this apparatus did not exist. It appears that the pedicle had atrophied in many of the middle and late Palaeozoic spiriferids and the pseudodeltidia or deltidia

were loosely attached to the palintrope, and consequently lost during fossilisation. A poorly preserved specimen in the writer's collections from Chimay (Belgium) has been identified as *Cyrtospirifer verneuili*. This specimen shows a triangular, convex pseudodeltidium, but does not show a pedicle perforation. This absence of a pedicle foramen is readily explained in terms of the degeneration of the pedicle. In view of the evidence presented, it does not appear reasonable to maintain *Cyrtiopsis* as a valid genus merely on its possession of a perforate pseudodeltidium.

Substantial differences between the two genera do, however, occur. The long convergent curved dental lamellae of *Cyrtiopsis* differ from the shorter divergent lamellae of *Cyrtospirifer*. *Cyrtiopsis* is also generally more brachythyrid and has a delicate but distinct micro-ornamentation consisting of radial striations. Crickmay has also shown that at least in North America the genus *Cyrtospirifer* is restricted to Frasnian equivalents, while *Cyrtiopsis* is restricted to Famennian equivalents. *Cyrtiopsis* must thus remain as a valid genus, but for different reasons to those advanced by the original author.

That *Theodossia* Nalivkin lies close to *Cyrtospirifer* was revealed by a study of the literature, and confirmed by the examination of specimens of *Theodossia hungerfordii* Hall from the Hackberry formation of Iowa. However, the two genera differ slightly in both macro-ornamentation and the shape of the fold and sinus. Despite the great variation in the shape and placement of the plications in *Cyrtospirifer*, there is a common basic design which is maintained throughout the genus. The bounding plications are the most pronounced and the lateral plications become finer towards the cardinal extremities. Plications are usually appreciably finer in the sinus, where they range in size according to their order of appearance. The sinus is not always well developed, but the bounding plications may be readily detected and the sinus can always be traced to the beak. The plications of *Theodossia* are finer than those of *Cyrtospirifer*. They increase in thickness from the cardinal extremities towards the sinus. It is always difficult and generally impossible to exactly delimit the boundary of the sinus of *Theodossia*, since the bounding plications do not differ appreciably from the plications of the flanks or the sinus. The sinus is shallow and is not developed until the animal has almost reached maturity. It is thus observed only in the anterior part of most shells, where it appears as a gentle undulation which gradually merges into the flanks. The nature of the sinus must have been related to the intensity of respiratory exchanges of the organism. Significant differences in the sinus of *Cyrtospirifer* and *Theodossia* have been demonstrated, and it is the opinion of the present author that these differences, together with the dissimilarity of the plications, warrant the retention of the two groups as separate genera.

TABLE IV
Measurements (in mm.) of Cyrtospirifer minilyaensis Glenister, n.sp.

Growth stage	Neanic		Ephebic		Gerontic
Catalogue number	457	458	459	460	477*
Plate	3—14—18	3—19—23	3—24—27	3—28—32	3—9—13
Figures	3—1	3—2	3—3	3—4	3—5
Height of pedicle valve	13.2	13.9	20.2	20.0	21.2
Length on curvature (centre)	14.3	15.7	23.0	24.5	25.1
Height of brachial valve	12.9	13.4	18.7	19.5	18.6
Length on curvature (centre)	15.5	15.7	25.0	24.0	22.9
Width along hinge line	24.0	23.0	25.7	27.0	25.4
Maximum width of shell	24.0	23.0	25.7	27.5	25.4
Maximum height of palintrope	4.9	4.6	5.2	6.0	7.3
Thickness of shell	8.8	9.2	14.5	15.6	13.9
Maximum width of sinus (anterior)	5.4	6.9	11.6	9.4	10.8
Number of lateral plications	30	26	28	30	28
Shell index of pedicle valve	1.70	1.47	1.12	1.10	1.01
Shell index of brachial valve	1.55	1.47	1.03	1.12	1.11

* Holotype

TABLE V
Shell indices for the pedicle valve of Cyrtospirifer minilyaensis Glenister, n.sp., measured on growth lines. Measurements in mm.

Catalogue number	477*						
Growth stage	Nepionic		Neanic		Ephebic		Gerontic
Length on curvature (centre)	6.0	9.1	14.0	15.4	19.8	23.2	25.1
Corresponding width along hinge line	10.9	16.2	22.4	22.8	25.2	25.3	25.4
Shell index	1.81	1.78	1.60	1.48	1.27	1.09	1.01

* Holotype.

Cyrtospirifer minilyaensis Glenister, n.sp.

Plate 3—9—32; figs. 3—1—5, 5—1—21; tables IV and V

Description.—The holotype, 2 paratypes, 4 hypotypes, and 95 other specimens belonging to this species were available to the author. The shells are inequally biconvex, the pedicle valve being deep and hemi-pyramidal and the brachial valve shallowly convex. Immature shells are much wider than long and have acutely angular cardinal extremities. Mature specimens are slightly wider than long, but are sub-quadrate with broadly rounded anterior-lateral margins and cardinal angles measuring slightly less than a right angle. The gerontic growth stage is marked by the development of small ears and the approach to unity of the shell index of the pedicle valve. In exceptional cases the greatest width may no longer lie along the hinge line. The anterior commissure is broadly uniplicate.

The pedicle valve is strongly arched laterally but only weakly convex along the plane of symmetry. The sinus is broad and shallowly rounded, extending from the point of the beak to the anterior margin, where it continues as a shallow rounded projection. The palintrope

is high, triangular, either flat or weakly concave, and apsacline in all growth stages. Growth lines parallel to the hinge line are frequently preserved, and a few well-preserved specimens show the area to be finely striated at right angles to the growth lines. A broad triangular delthyrium, having its apex immediately below the beak, bisects the palintrope. Apparatus for closing the delthyrium is not preserved in any of the specimens in the author's collections.

The brachial valve is flatly convex with shallowly concave posterior-lateral margins. The umbo is weakly developed and partially overhangs a low cardinal area which is bisected by a broad notothyrium and is generally orthocline. A weakly convex fold extends from the beak to the anterior margin, where it is truncated by the sinial extension of the pedicle valve.

The dental lamellae are thin and diverge anteriorly along the floor of the pedicle valve for slightly more than a third of the distance to the anterior margin of the conch. They support two strong teeth. The area of muscle attachment is crossed by fine radially-directed striations and bears a median fold at the posterior end. Lines of growth in the dental lamellae show that they are composed of two distinct elements. The growth lines of the outer layer

are continuous with those of the shell, while those of the inner layer join through the subdelthyrial platform. This subdelthyrial platform joins the dental lamellae near their posterior ends, just above their mid-height. Its dorsal surface is flatly concave and the ventral surface markedly concave. Three rostral cavities are present in all growth stages, one beneath the delthyrial platform and one on either external side of the dental lamellae.

The area of muscle attachment of the brachial valve is smaller than in the pedicle valve. The external branch of each adductor muscle leaves a narrow curved scar. Anterior to these the internal branches of the adductors were attached to the shell in a pair of broad deep pits separated by a median ridge. The cardinal process is well-developed, consisting of a series of fine lamellae. The socket plates are thick but unsupported by lamellae. They surround deep narrow dental sockets. The descending lamellae are straight and converge anteriorly to the points of attachment of the posterior-laterally-directed spires.

Each valve is covered with radially-directed plications, those on the flanks being invariably simple while the plications of the fold and sinus may show bifurcations and intercalations. The number of lateral plications on either flank varies between 26 and 30 for mature specimens. Sinus plications are much more variable in number, ranging from 9 to 13. The plications which bound the sinus are more pronounced than any others. In the posterior portion of the inside of the valves, weak imprints of the external plications and growth lines are frequently encountered. Growth lines are numerous and occasionally lamellose, especially in the gerontic stage.

The species is named after the Minilya River.

Comparisons.—Like the other species of *Cyrtospirifer* to be described later, *Cyrtospirifer minilyaensis* is closely comparable although not specifically identical with some of the species described by Grabau (1931) and Tien (1938) from the Upper Devonian of southern China. The combination of hemi-pyramidal pedicle valve, high flat umbo and subquadrate shell outline distinguish *Cyrtospirifer minilyaensis* from other Western Australian species.

Occurrence.—Holotype No. 477 is from locality 178, paratypes Nos. 437-438 from locality 207, hypotypes Nos. 457-458 from locality 180, and hypotypes Nos. 459-460 from locality 181 in the Gneudna Limestone, 3.4 miles south of Gneudna Well, Williambury Station, North-West Basin, Western Australia.

Repository.—All types are lodged with the Bureau of Mineral Resources, Geology and Geophysics, Canberra.

Cyrtospirifer australis Glenister, n.sp.

Plate 4—1-24; Plate 5—1-5; figs. 2—1-15.

3—7-9, 4—1-14; tables VI and VII

Description.—The holotype, 3 paratypes, 5 hypotypes and 250 other specimens of *Cyrtospirifer australis* were available to the author. The shell is sub-equally biconvex with the pedicle valve generally showing a slightly greater convexity, especially in mature and gerontic stages. Immature specimens may be twice as broad as they are long, and have their cardinal extremities produced into angular ears. As maturity is approached the ratio of the width to length approaches unity, and gerontic specimens may become brachythyrid and subrectangular in outline. Obesity is a gerontic feature. The anterior commissure is broadly uniplicate.

TABLE VI

Measurements (in mm.) of *Cyrtospirifer australis* Glenister, n.sp.

Growth stage	Nepionic	Neanic	Ephebic		Gerontic	
Catalogue number	461	462	427*	463	464	465
Plate	4—6-9	4—10-14	4—1-5	4—15-19	4—20-24	5—1-5
Figures	3—7	3—8	3—9
Height of pedicle valve	22.6	20.2	31.8	26.0	27.5	31.0
Length on curvature (centre)	28.0	24.0	44.8	36.5	40.5	43.0
Height of brachial valve	21.4	18.0	27.9	23.4	26.3	27.0
Length on curvature (centre)	26.5	22.3	37.0	30.6	33.5	35.5
Width along hinge line	34.1	26.2	45.6	33.2	33.4	33.1
Maximum width of shell	34.1	26.2	45.6	33.2	33.4	34.7
Maximum height of palintrope	5	4	7	5	7
Thickness of shell	15.4	13.1	23.7	18.5	22.0	23.6
Maximum width of sinus (anterior)	13.9	9.8	15.0	15.6	14.8	14.5
Number of lateral plications	32	30	33	34	32	33
Shell index of pedicle valve	1.22	1.09	1.02	0.91	0.82	0.77
Shell index of brachial valve	1.29	1.13	1.23	1.08	1.00	0.93

* Holotype.

The pedicle valves of immature specimens are arched more strongly along the plane of symmetry than transversely. The flanks are either flat or slightly concave. Mature and gerontic specimens have flanks which are convex except for a small area adjacent to the cars. A broad, shallow, uniformly-rounded sinus extends from the beak to the anterior shell margin, where it continues as a low projection. The junctions between the sinus and the flanks are broadly rounded. The umbo of the pedicle valve is a prominent conch feature and is never appreci-

ably recurved. The palintrope is high and sub-triangular. Its height is partially maintained laterally by the development of shelf-like projections from the lateral slopes, particularly in the vicinity of the cardinal extremities. In immature specimens the palintrope is practically flat but in mature and gerontic individuals it is gently concave. It is apsacline in all growth stages. Growth lines parallel to the hinge line may be observed in well-preserved specimens. A flatly triangular delthyrium bisects the palintrope.

TABLE VII

Shell indices for the pedicle valve of Cyrtospirifer australis Glenister, n.sp., measured on growth lines. Measurements in mm.

Catalogue number	465											
Growth stage	Nepionic				Neanic		Ephebic		Gerontic			
Length on curvature (centre)....	4.5	8.0	10.4	14.8	19.0	22.5	28.0	31.2	34.2	38.5	43.0	
Corresponding width along hinge line	9.6	18.2	21.6	27.8	29.6	31.4	31.9	32.4	32.8	33.0	33.1	
Shell index	2.13	2.27	2.08	1.88	1.56	1.40	1.44	1.04	0.96	0.86	0.77	

A considerable area of the posterior-lateral flanks of the brachial valve is flat or concave in all growth stages. Pedicle valves are invariably more strongly arched along the mid-line than in the lateral direction, especially in immature specimens. The fold is only slightly elevated and may be weakly convex, flat, or even weakly concave. It is truncated anteriorly by the sinal projection of the pedicle valve. The umbo is weakly developed. The area projects as a narrow shelf and is apsacline in all growth stages.

Internally, the pedicle valve has two dental lamellae which extend along the floor of the valve for two-thirds of the distance towards the anterior shell margin. They directly support the teeth. The dental lamellae diverge anteriorly. A low median septum traverses the posterior half of the longitudinally-ridged area of muscle attachment. The structural lines in the calcite of the dental lamellae show the latter to be made up of two layers. The outer layer has growth lines continuous with those of the outer shell material while the internal layer shows growth continuity with the sub-delthyrial platform. This sub-delthyrial platform is a plano-concave horizontal plate which joins posterior parts of the dental lamellae above their mid-height, leaving a pronounced cavity beneath it. Secretion of shell material may tend to obliterate these finer structures of the rostral area, but this process is never carried to the point where the structures mentioned above are not readily discernible.

The socket plates of the brachial valve are thick and unsupported by lamellae. To them are attached the fine descending lamellae. The descending lamellae are at first straight, and slowly converge anteriorly. Near their mid-length they become curved towards each other and converge rapidly until they lie close together at their points of attachment to the posterior-laterally directed spires. The length of

the area of muscle attachment of the brachial valve is about one-half the length of the valve. The muscles were attached to the bottom of a shallow pit traversed by a median ridge. The cardinal process consists of numerous lamellae of 0.1 mm. thickness, spaced 0.1 mm. apart. These lamellae are disposed in vertical planes radiating from the beak.

Both valves bear from 30 to 34 radial plications on either side of the fold or sinus. The number of sinal plications varies with age of the individual, the average for mature individuals being about 14. Lateral plications are invariably simple, but frequent bifurcation and intercalation characterizes the sinal plications. The plications are narrower than the furrows which separate them. Well-preserved specimens bear fine longitudinal striations in the furrows, and it is assumed that these were also present on the plications. Sinal plications are generally finer than the laterals. The plications of the sinus are usually arranged asymmetrically due to a relative retardation in development of one side with respect to the other.

Comparisons.—This species is distinguished by the numerous and complex plications of the sinus, large size, subquadrate margin, and relatively narrow concave palintrope.

Occurrence.—Holotype No. 427, paratypes Nos. 439-440 and hypotypes Nos. 461-465 are from locality 17 and paratype No. 441 is from locality 177 in the Gneudna Limestone, Williambury Station, North-West Basin, Western Australia. Locality 17 lies 1.75 miles north of Gneudna Well, and locality 177 lies 3.5 miles south of Gneudna Well.

Repository.—All types are lodged with the Bureau of Mineral Resources, Geology and Geophysics, Canberra.

Cyrtospirifer gneudnaensis Glenister, n. sp.

Plate 5—6-27; Plate 6—1-20; Figs. 1—5-10, 4—15-18; Tables VIII and IX.

Description.—The holotype, two paratypes, seven hypotypes and 70 other specimens of *Cyrtospirifer gneudnaensis* were available to the author. Nepionic shells are spiriferoid, wider than long, and show acutely angular alate cardinal extremities. As maturity is approached,

the cardinal extremities become subrectangular and the greatest width no longer lies along the hinge line, but along a line approximately half-way between the anterior and posterior margins. The gerontic stage is marked by obesity, still further anterior movement of the line of greatest width, and a marked increase in the incurvature of the ventral umbo. The anterior commissure is weakly uniplicate.

TABLE VIII

Measurements (in mm.) of Cyrtospirifer gneudnaensis Glenister, n.sp.

Growth stage	Nepionic		Neanic		Ephebic		Gerontic	
Catalogue numbers	466	467	468	469	428*	470	471	472
Plate	5—14-18	5—19-22	5—23-27	6—1-5	5—6-10	6—6-10	6—11-15	6—16-20
Figures	1—5	1—6	1—7	1—8	1—9	1—10
Height of pedicle valve	18.1	17.0	23.4	22.0	24.7	25.0	24.5	30.0
Length on curvature (centre)	25.0	22.5	34.0	32.5	35.0	35.0	40.5	49.5
Height of brachial valve	16.6	15.8	21.6	19.9	22.2	22.7	22.2	26.4
Length on curvature (centre)	20.5	18.0	27.0	24.0	26.0	27.0	28.5	35.5
Width along hinge line	28.4	22.5	29.3	26.2	27.8	23.4	24.2	27.0
Maximum width of shell	28.4	22.5	29.3	26.2	28.2	26.0	26.9	28.6
Maximum height of palintrope	2	2	3	3	3	3	3
Thickness of shell	11.6	10.4	16.9	15.4	17.0	16.2	19.8	24.6
Maximum width of sinus (anterior)	9.0	7.0	12.3	9.2	12.0	13.0	13.0	13.5
Number of lateral plications	28	26	28	27	28	27	28	28
Shell index of pedicle valve	1.14	1.00	0.86	0.80	0.79	0.67	0.60	0.56
Shell index of brachial valve	1.39	1.25	1.09	1.09	1.07	0.87	0.85	0.79

* Holotype.

The pedicle valve is strongly arched with the sharpest convexity in the region of the umbo. Immature specimens are flat or weakly concave along the posterior-lateral margins. A shallow, uniformly rounded sinus originates at the beak and increases rapidly in width and depth towards the anterior margin, where it projects as a low rounded extension. The umbo of the pedicle valve is strongly developed and gives rise to a sharply pointed beak. In gerontic forms, the incurvature of the beak is increased to the extent that it completely overhangs the palintrope and almost comes into contact with the weakly-developed umbo of the brachial valve. The palintrope is narrow and gently concave, ranging from apsacline in nepionic specimens to anacline in gerontic forms. It is bisected by a broad low delthyrium. Fine longitudinal stria-

tions are observed on the the palintrope of well-preserved specimens.

The brachial valve is less strongly arched than the pedicle valve, and in all but gerontic specimens shows flattened or gently concave posterior-lateral margins. In immature specimens this valve is more narrowly arched along the mid-line than in a lateral direction. Gerontic specimens show the curvature to be equal in both directions. The fold of the brachial valve is weakly developed; in most specimens it appears as a flattening in the shell curvature rather than a true elevated fold. It is truncated anteriorly by the lingual extension of the pedicle valve. The umbo is broad and low, and the beak poorly developed. The area is narrow and gently apsacline in all growth stages. It is bisected by a low broad notothyrium.

TABLE IX

Shell indices for the pedicle valve of Cyrtospirifer gneudnaensis Glenister, n.sp., measured on growth lines. Measurements in mm.

Catalogue number	428*				471†							
	Nep.		Nea.	Eph.	Nep.		Nea.		Eph.		Ger.	
Length on curvature (centre)	21.0	25.8	30.5	35.0	12.2	18.0	20.8	24.8	28.6	34.1	36.6	40.5
Corresponding width along hinge line	25.6	26.7	27.6	27.8	19.4	23.4	23.5	23.7	23.9	24.1	24.2	24.2
Shell index	1.22	1.03	0.90	0.79	1.59	1.30	1.13	0.95	0.84	0.71	0.66	0.60

* Holotype.

† Paratype.

The dental lamellae extend anteriorly along the floor of the ventral valve from the posterior valve margin half-way to the anterior margin. Closely-spaced longitudinal striations cover the muscle pit, and a pronounced median septum extends anteriorly, from beneath the subdelthyrial platform for one-third the length of this pit. The subdelthyrial platform is weakly developed. A shallow rostral cavity is formed between the dental lamellae as well as on the lateral side of each dental lamella. These cavities may be obliterated in the mature and gerontic growth stages by secretion of shell material in the rostral area.

The area of muscle attachment in the brachial valve is slightly smaller than in the pedicle valve. The muscle pit is traversed by a few coarse ridges; a deep groove surrounds the muscle scars. The socket plates are thick. They support the fine descending lamellae to which the brachidium is attached. Each spire of the brachidium is directed posterior-laterally. The cardinal process consists of shell lamellae 0.1 mm. in thickness spaced 0.1 mm. apart. Up to 20 of these lamellae may be seen radiating from the beak.

Both valves bear radial plications. Mature specimens have 27 or 28 plications on either side of the sinus; the number in the sinus is more variable but averages about 10. Lateral plications are invariably simple, but those in the sinus often show bifurcation and intercalation. The plications are narrower than the furrows, the sides almost vertical, and the crests either flat or gently rounded. Well-preserved specimens bear filamentous radial striations in the furrows and it is assumed that these were also present on the plications. The bottoms of the furrows are gently rounded. The bounding plications, on either side of the sinus, are the widest. The sinus is not always symmetric-

ally plicated, one side often being more retarded than the other. When this relative retardation is observed, bifurcations and intercalations which occur on the advanced side do not occur on the retarded side.

The species is named after the Gneudna Limestone.

Comparisons.—The pedicle valve of *Cyrtospirifer gneudnaensis* is shallower and has a much narrower interarea than other Western Australian species of this genus.

Occurrence.—Holotype No. 428 and hypotypes Nos. 468 and 472 came from locality 27/8 B, paratype No. 442 from locality 177, paratype No. 443 from locality 178, hypotypes Nos. 466-467 and 469-471 from locality 177. All these localities lie in the Gneudna Limestone approximately 3.5 miles south of Gneudna Well, Williambury Station, North-West Basin, Western Australia.

Repository.—All types are lodged with the Bureau of Mineral Resources, Geology and Geophysics, Canberra.

Cyrtospirifer brevicardinis Glenister, n.sp.

Plate 6—21-25: figs. 3—6, 6—1-16; Table X.

Description.—The holotype, one paratype and one other specimen belonging to this species were available for study. The shell is inequally biconvex, the pedicle valve being deeper than the brachial valve. Growth lines show that in the neanic growth stage, the hinge line represented the widest part of the shell, and had a width which was greater than the length (measured along the surface of the pedicle valve in the plane of symmetry). The shells are brachythyrid in the ephebic and gerontic growth stages. The cardinal extremities are never mucronate and ears are not developed. The anterior commissure is strongly uniplicate.

TABLE X

Shell indices for the pedicle valve of Cyrtospirifer brevicardinis Glenister, n.sp.
measured on growth lines. Measurements in mm.

Catalogue number	429*										
Growth stages	Neanic			Ephebic				Gerontic			
Length on curvature (centre)	10.5	12.5	18.1	23.2	28.3	31.7	35.0	35.9	37.7	39.0	40.7
Corresponding width along hinge line	14.1	15.0	16.3	16.7	17.4	18.9	20.6	20.7	20.8	20.9	20.9
Shell index	1.34	1.20	0.9	0.72	0.62	0.60	0.59	0.58	0.55	0.54	0.51

* Holotype.

The pedicle valve bears a deep sinus. It extends from the tip of the beak to the anterior margin of the valve, where it forms a prominent projection which truncates the fold of the brachial valve. The umbo is strongly developed, the sharply pointed beak overhanging the uniformly concave palintrope. The palintrope is traversed by numerous growth lines running parallel to the hinge line. The broadly triangular delthyrium is partially closed by an imperforate pseudodeltidium which occupies the apical half of the delthyrium.

The fold on the brachial valve is low but is well defined by the two deep costae which bound it. The interarea is narrow, flat, and orthocline.

Internally, the pedicle valve possesses two thick dental lamellae which are attached to the floor of the valve for about half of its length. These dental lamellae gradually diverge anteriorly. They are joined below the level of the hinge line by a subdelthyrial platform. A deep rostral cavity appears on either side of the dental lamellae and also between

them; the lateral cavities are roofed by the palintrope, and the medial cavity by the sub-delthyrial platform. The internal structures of the rostral area tend to be obscured in the gerontic growth stage by secretion of shell material.

The socket plates of the brachial valve are thick and unsupported. To them are attached the descending lamellae. These are thin and converge slowly anteriorly to near the points of attachment of the posterior-laterally directed spires of the brachidium. A low median septum appears on the posterior half of the floor of the brachial valve.

The valves bear about 20 radial plications on either side of the fold and sinus. In no case has bifurcation or intercalation of these plications been observed. The fine longitudinal striations which cover the grooves between the plications of other Western Australian species of *Cyrtospirifer* have not been found in this species. This may be due to relatively poor preservation of the few specimens available for study. Sinal plications are finer than those on the flanks adjacent to the sinus. The holotype bears 10 simple sinal plications. Primary sinal plications are indistinguishable from the primitive plications of the sinus.

The species name refers to the brachythyrid shell outline.

Comparisons.—*Cyrtospirifer brevicardinis* differs from all other Western Australian species of *Cyrtospirifer* in its markedly concave palintrope, recurved umbo and brachythyrid shape in all but the earliest growth stages.

Occurrence.—Holotype No. 429 came from locality 194 and paratype No. 478 from locality 27/8 AA in the Gneudna Limestone, William-bury Station, North-West Basin, Western Australia. Both localities lie approximately 3.5 miles south of Gneudna Well.

Repository.—All types are lodged with the Bureau of Mineral Resources, Geology and Geophysics, Canberra.

Carboniferous

Subfamily *Spiriferinae* Schuchert, 1913

Genus *Spirifer* Sowerby, 1814

Spirifer fluctuosus Glenister, n. sp.

Plate 7—1-14; plate 8—1-8

Description.—The holotype, 4 paratypes and over 200 specimens belonging to this species were available to the author. Most of the specimens occur as single silicified valves with slightly damaged anterior margins. The shells are spiriferoid with mucronate cardinal extremities in all growth stages. The valves are sub-equally biconvex, the pedicle valve being slightly more convex than the brachial. The anterior commissure is shallowly uniplicate. The shell is completely plicate. Broad, low, rounded plications radiate from the beak across the flanks.

These lateral plications are invariably simple, bifurcation never having been observed. Bifurcation of the plications is common in the fold and sinus. About 25 plications are present on either flank of the holotype and an average of five plications occur in the sinus.

A shallow but distinct sinus traverses the pedicle valve from the beak to the anterior margin, where it extends as a low rounded projection which truncates the fold of the brachial valve. The umbo of the pedicle valve is slightly recurved so as to slightly overhang the palintrope. The palintrope is high, concave outwards and anacline in position through all growth stages. Ornamentation consists of growth lines parallel to the hinge line and denticle grooves at right angles to it. The denticle grooves frequently bifurcate and anastomose. They are continuous with sharply-pointed denticles along the hinge line. These denticles articulate with a row of shallow denticle pits in the palintrope of the brachial valve. Denticles first appear close to the teeth and extend along the hinge line to the cardinal extremities. A flatly-triangular delthyrium bisects the palintrope. The width of the delthyrium, measured along the hinge line, is slightly greater than its height. Apparatus for closing the delthyrium is not known. A narrow groove is present in the palintrope on either side of the delthyrium.

Immature pedicle valves have a pair of dental lamellae traversing about a quarter of the distance from the rostral area to the anterior valve margin. They are continuous with the base of the teeth and diverge slowly anteriorly along the floor of the valve. Just above their mid-height they are joined by a prominent sub-delthyrial platform. In immature specimens there are thus three rostral cavities. A central cavity occurs below the sub-delthyrial platform, and there are two lateral cavities, one situated laterally to each of the two dental lamellae. Maturity is evidenced by the development of a thick apical callosity. The two lateral cavities are completely obliterated, but the central cavity is retained in a reduced state. A median septum extending along the floor of the pedicle valve one-fifth of the distance to the anterior margin is present in all growth stages but is never pronounced. It gives place anteriorly to a broad shallow median groove which separates the two oval muscle scars. These muscle scars attain almost half the length of the valve. The muscle scars are radially crenulated, the focus of the crenulations being at the point where the median septum gives place to the median groove.

A low fold traverses the brachial valve from the beak to the anterior margin, where it is truncated by an extension of the sinus in the pedicle valve. The umbo of the brachial valve is small and the beak bluntly pointed. The dorsal palintrope is anacline in attitude near the cardinal extremities, but becomes orthocline and finally apsacline, towards the umbo. Close to the sockets, the line of denticle pits is situated at the anterior edge of the palintrope. From the sockets outwards this line of denticles diverges posteriorly from the anterior edge of

the palintrope, so that at the cardinal extremities the denticle pits lie almost in the centre of the palintrope. The socket plates are thick and directly supported by the posterior wall of the brachial valve. The sockets are deep, long and narrow. They decrease gradually in width as they converge towards the beak. At their posterior extremities they bound the finely-laminated cardinal process. The individual lamellae of the cardinal area are about twice the thickness of the interspaces which separate them. In paratype No. 444, there are 34 such lamellae in a cardinal process of 2.6 mm. width. Individual lamellae thus average 0.05 mm. in thickness. A median septum is present, stretching along the floor of the brachial valve from the rostral area one-third the distance to the anterior valve margin. The muscles were lodged in two pairs of oval pits on either side of the median septum. Occasional specimens show the inner shell surface of the posterior half of the valve to be covered by shallow rounded pits about 0.5 mm. in diameter.

The species name refers to the crenulation of the anterior margin of the palintrope in the ventral valve.

Comparisons.—*Spirifer fluctuosus* is closely comparable with *Spirifer striata* Martin the type species of the genus. The Western Australian species may be distinguished readily since it has fewer sinal plications, and the plications across the flanks are invariably simple.

Occurrence.—All types came from locality 1949/42 in the Moogooree Limestone, 3.5 miles north-west of Gneudna Well, Williambury Station, North-West Basin, Western Australia.

Repository.—Holotype No. 430, and paratypes Nos. 444-446 and 479 are lodged with the Bureau of Mineral Resources, Geology and Geophysics, Canberra.

Subfamily *Spiriferininae* Schuchert and
Le Vene, 1929

Genus *Punctospirifer* North, 1920

Punctospirifer plicatosulcatus Glenister, n.sp.
Plate 6—26-29; plate 8—10-12

Description.—The holotype, 1 paratype and 70 specimens belonging to this species were available to the author for study. The shell is biconvex, the pedicle valve being hemi-pyramidal and the brachial valve flatly convex. The hinge line represents the greatest width of the shell in all growth stages. Immature forms are spiriferoid, but as maturity is reached, the length (measured along the curvature, in the plane of symmetry) equals and then exceeds the width along the hinge line. The anterior commissure is broadly sulcate.

The holotype is a pedicle valve. The width of the hinge line is 18.5 mm., the length of the shell 19.5 mm., and the maximum height of the

palintrope 5.9 mm. The palintrope is gently concave and apsacline in all growth stages. It is bisected by a large triangular delthyrium, which has its apex immediately below the beak, and reaches a maximum width of 4.9 mm. along the hinge line. A narrow groove appears in the palintrope on either side of the delthyrium, but although these grooves probably lodged the edges of the delthyrial covering apparatus, this apparatus has not been observed. The palintrope is crossed by numerous growth lines parallel to the hinge line. A broad shallow sinus is present on the pedicle valve. At the anterior border this sinus is extended as a tongue-shaped projection which truncates the fold of the pedicle valve. A pair of prominent dental lamellae are present in the rostral area. They diverge towards the floor of the valve where they run parallel to the radial plications of the shell. The dental lamellae extend from the posterior shell margin for one-third of the distance to the anterior margin. A prominent median septum traverses the posterior half of the floor of the valve. The rostral callosities so characteristic in the mature shells of many spiriferids are unknown in this species.

The palintrope of the brachial valve is extremely narrow. A low rounded fold is present. The socket plates are attached to the posterior wall of the shell on either side of the laminated cardinal process. The brachidium is not preserved in any of the specimens available for study, but the posterior extremities of the descending lamellae are often preserved. They appear as large but narrow plates attached to the socket plates.

The flanks of both valves are crossed by rounded plications. Nine are present on either flank of the holotype. A single poorly-developed plication occurs in the plane of symmetry of the sinus of the pedicle valve, and the supplementary groove is present on the fold of the brachial valve. The surface of both valves is traversed by regularly-disposed concentric imbricating lamellae. Numerous endopunctae are present in both valves.

The species name refers to the single sinal plication.

Comparisons.—*Punctospirifer plicatosulcatus* lies close to *Punctospirifer scabricosta* North, type species of *Punctospirifer* from the lower part of the *Productus corrugato hemisphericus* Zone (Zone 5) of the Ashfell Sandstone. The Western Australian species differs from all other species of *Punctospirifer* in the presence of a median plication in the sinus of the pedicle valve.

Occurrence.—Holotype No. 431 came from locality 1950/42 and paratype No. 447 from locality 1949/42 in the Moogooree Limestone, Williambury Station, North-West Basin, Western Australia. Both localities lie approximately 3.5 miles north-west of Gneudna Well.

Repository.—The type material is lodged with the Bureau of Mineral Resources, Geology and Geophysics, Canberra.

Genus *Syringothyris* Winehell, 1863

Syringothyris spissus Glenister, n. sp.

Plate 7—15; plate 8—9; fig. 7—1-13

Description.—The holotype, 2 paratypes and about 50 other specimens belonging to this species were available to the author. Most of the specimens represent only the rostral area of the pedicle valve; the more delicate anterior half of the pedicle valve and the whole of the braehial valve were apparently destroyed during fossilization. Many of the specimens are wholly or partially silicified, but several show little or no silicification and are in an almost perfect state of preservation.

The holotype of *Syringothyris spissus* consists of the posterior halves of both valves of a well-preserved specimen. The shell is spiriferoid in form and biconvex, the braehial valve being flatly convex and the pedicle valve hemipyramidal. The hinge line is straight. It represented the greatest width of the shell in all growth stages. The shells are impunctate.

A deep, uniformly-rounded sinus is present in the pedicle valve, extending from the beak anteriorly. The sinus is smooth, but the flanks are covered with simple radial plications. Neither bifurcation nor intercalation of these plications have been observed in the specimens available to the author. The palintrope is high and almost flat. It is slightly concave in the vicinity of the beak. Ornamentation of the palintrope consists of growth lines parallel to the hinge line, and in a few specimens fine striations running at right angles to the hinge line are observed. In the few specimens of *Syringothyris spissus* in which these fine striations (at right angles to the hinge line) are known, they invariably occur close to the delthyrium. The palintrope is bisected by a triangular delthyrium with a length equalling almost three times its greatest width. A shallow narrow groove occurs in the palintrope on either side of the delthyrium. The apparatus for closing the delthyrium has not been preserved in any of the specimens studied.

A pair of strongly-developed dental lamellae are present in the pedicle valve. They extend from the posterior margin of the valve to the base of the teeth, and diverge to the floor of the valve where they traverse about a quarter of the distance to the anterior shell margin. They are joined just above their mid-height by a subdelthyrial platform. Serial sections of the rostral area show that the dental lamellae consist of two components. The outer component is continuous with the palintrope and the shell, while the inner component bends inwards to form the subdelthyrial platform. At its anterior margin the subdelthyrial platform is extended anteriorly to form a tube-like process, the syrinx. The syrinx is formed by two plates growing ventrally from the base of the subdelthyrial platform and curving inwards until they meet and form a tube. A narrow groove occurs where the two plates meet on the ventral side of the syrinx, and a narrow ridge appears dorsally. The dorsal ridge is well-developed on the syrinx but becomes

ill-defined and eventually disappears on the dorsal surface of the subdelthyrial platform. On the holotype the inside of the syrinx is longitudinally grooved at its anterior end. It appears that the inside of the syrinx is composed of radially-arranged thin lamellae of calcite, similar to, though much coarser than, the lamellae which make up the cardinal processes of many spiriferids. The lamellae extend 4 mm. posteriorly from the anterior end of the syrinx on the dorsal side, and 2 mm posteriorly on the ventral side. In most specimens this laminated portion of the syrinx is missing. This is readily explained when it is realised that in the Western Australian species, the rostral area of the pedicle valve was strong and heavy, whereas the rest of the shell was comparatively fragile. Most specimens were evidently fractured soon after the death of the animal and the rostral area separated from the rest of the shell. The syrinx would then constitute a fragile salient which was easily damaged. The laminated nature of the internal portion of the syrinx lends strong support to the suggestion that it served as an area of muscle attachment. An ill-defined median septum is present in the posterior half of the pedicle valve. This septum separates a pair of large oval muscle scars. The muscle scars are radially erenulated, the focus of the crenulations being situated on the median septum.

The braehial valve bears a low but distinct fold. The fold is smooth, but the flanks bear numerous radial plications. The socket plates are in close contact with the posterior shell wall and the sockets consist of deep narrow trenches. A weakly-developed median septum occurs in the braehial valve. The cardinal process is made up of numerous fine lamellae. The nature of the brachidium is unknown.

The species name refers to the impunctate nature of the shell.

Comparisons.—With the exception of the non-punctate shell structure, the species under discussion is a typical member of Winehell's genus *Syringothyris*. A detailed examination of the shell structure has convinced the author that the species is indeed non-punctate. The fauna came from what must have originally been a fairly pure limestone. Since Carboniferous times the fossil content of the limestone has been partially silicified, and a superficial examination of the material might suggest that silicification has obliterated the punctae. However, completely silicified specimens of *Punctospirifer plicatosulcatus* from the same beds invariably show well-preserved and very obvious punctae. It might be argued that the punctae of *Syringothyris* are generally finer than those of *Punctospirifer*. The two paratypes of the Western Australian species represent sections through the posterior third of the pedicle valve. In these specimens only a thin layer on either side of the shell wall has been silicified. Thin sections show minute detail in shell structure up to 180 diameters but no trace of punctation has been observed. There can be no doubt that this species is impunctate, but in all other morphological features it is a typical *Syringothyris*.

It is difficult to believe that a complex structure such as the syrinx could appear simultaneously in two fundamentally different spiriferid groups (punctate and impunctate). The fact that both punctate and impunctate syrinx-bearing forms do appear simultaneously shows clearly the inadequacy of a classification which accepts the presence or absence of punctae as of primary taxonomic importance. As indicated earlier in this paper, the author is of the opinion that the presence or absence of punctae in the spiriferids is of secondary importance. For this reason it is proposed that the species

under discussion be assigned to *Syringothyris* and that this genus be expanded to include impunctate forms.

Occurrence.—Holotype No. 432 and types Nos. 448 and 480 came from locality 153 in the Moogooree Limestone, 2.5 miles north-west of Gneudna Well, Williambury Station, North-West Basin, Western Australia.

Repository.—All types are lodged with the Bureau of Mineral Resources, Geology and Geophysics, Canberra.

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